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Mountain Pine Beetle in Colorado: A Story of Changing Forests

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The mountain pine beetle (MPB) (*Dendroctonus ponderosae*) is one of the most prevalent disturbance agents in western conifer forests. It utilizes various species of pines (*Pinus* spp.) as host trees. Eruptive populations can cause extensive tree mortality. Since the late 1990s, extensive outbreaks have occurred from the southern Rockies to British Columbia. In Colorado, lodgepole pine (*P. contorta*) forests have been the most affected. Since 1996, about 3.4 million acres of lodgepole and ponderosa pine (*P. ponderosa*) forests have exhibited MPB-caused tree mortality. A large portion of the larger diameter trees have been killed with significant reductions in basal areas and tree densities. Tree mortality has impacted many forest ecosystem services including fiber production, hydrology, nutrient cycling, wildlife habitat, property values, and recreation. In this article, we examine and summarize some of what we have learned about MPB impacts from observations and research over the past two decades in Colorado.

Keywords: *Dendroctonus ponderosae*, *Pinus contorta*, bark beetles, mountain pine beetle, lodgepole pine

The Colorado Mountains are among the most beautiful parts of the country where millions visit and recreate. But over the past two decades, expanses of once green mountains became reddish-orange and gray as dead trees shed their needles. From the late 1990s to 2012, nearly 3.4 million acres of forest were affected in Colorado (Colorado State Forest Service 2014). Yet, what seems like a sad story is actually a tale of changing forests resulting from an eruptive population of the native mountain pine beetle (*Dendroctonus ponderosae*) (MPB). The insect utilizes species of pines (*Pinus* spp.) as hosts, with lodgepole pine (*P. contorta*) and ponderosa pine (*P. ponderosa*) as the most abundant in Colorado. The historical distribution of MPB comprises southern British Columbia and then goes east to South Dakota and south to Baja California, Arizona, and New Mexico (Wood 1982).

Primary ecosystem services provided by Colorado's forests are water and recreation. Forests cover about 24.4 million acres, 11.3 of which million are managed by the USDA Forest Service, and 7.1 million are privately owned. Lodgepole and ponderosa pine forests comprise about 1.7 and 2.5 million acres, respectively (Colorado State Forest Service 2011). In Colorado's northern Front Range, MPB mortality occurred primarily in lodgepole pine, attracting national and local media attention and concerns over public safety, threats to lives, homes, infrastructure from falling trees, risk of fires, potential devaluation of properties, and impacts on recreation. By 2005, residents and communities were organizing cooperatives with local governments to address finances and logistics to deal with the epidemic. For example, in 2005 the Northwest Colorado Council of Governments and US Forest Service leaders formed the Colorado Bark Beetle Cooperative (CBBC) to advocate for state and federal attention to the growing epidemic (http://nwccog.org/programs/rural-resort-region/cbbc, last accessed June 2018). Initially the CBBC consisted of three National Forest Supervisors, the Colorado State Forester, six county commissioners, and various local community officials. The group expanded to include additional counties, water and power utilities, wood products companies, and other nongovernmental organizations (Abrams et al. 2017). As the epidemic moved into mountain towns, social license to cut and remove infested trees increased. The town of Frisco in Summit County held a Main Street festival called "Beetle Fest" that provided entertainment and education about the MPB and featured "wood carving to bug eating and all points in between" as an annual event from 2008 to 2011.

To protect high-value trees on developed sites, communities, individuals, and federal landowners used insecticides, which are highly effective to prevent attacks by MPB (Fettig et al. 2006). Although less effective,

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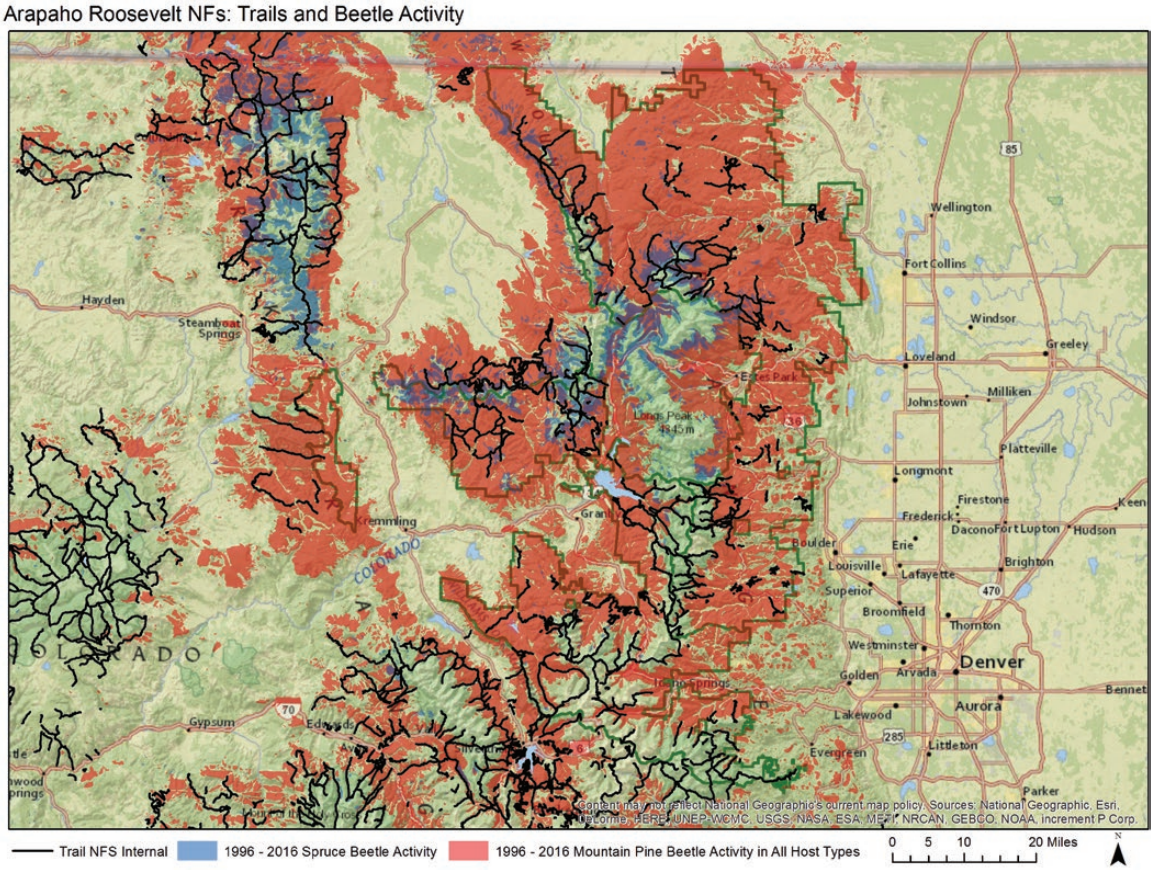

Figure 1. Hiking trails in the Arapaho-Roosevelt NF in northern Colorado and surrounded by bark beetle–caused tree mortality, Arapaho-Roosevelt NF. 1996–2016, USDA FS, Rocky Mountain Region. Forest Health Protection. 2017.

many areas were treated with commercial formulations of verbenone, an insect- and microbial symbiont-produced anti-aggregation pheromone to disrupt MPB attacks. Mostly on private lands, infested trees were treated using solar radiation, chipping, debarking, or burning to kill MPBs or were removed for wood products.

Why Was This Outbreak So Severe?

Three primary factors have been associated with the outbreak in north central Colorado. First, large, contiguous, overstocked stands of large-diameter trees increased the likelihood and size of MPB infestations (Negrón and Klutsch 2017). Forest Inventory data for Colorado from 2002–09 indicate that 87 percent of the lodgepole pine acreage was comprised of 41 percent sawtimber (trees > 8.9 inches) and 48 percent of poletimber (trees 5.0 – 8.9 inches) (https://www.fia.fs.fed.us, last accessed April 2018) representing an abundance of susceptible-sized trees. Second, a significant drought likely stressed trees, increasing susceptibility to MPB (Creeden et al. 2014, Kolb et al. 2016). The Palmer Drought Severity Index in northern Colorado in 2001–03 ranged from −3 to −6, representing severe drought conditions (http://www.ncdc.noaa.gov/cag, last accessed December 2007). Third, warm winter temperatures may have fostered higher survival of overwintering MPB populations. Cold winter temperature is a key mortality agent of MPB (Wygant 1938, Amman 1973). Winter low temperatures have been warmer since about 1980 in northern Colorado compared with previous decades, likely fostering increased winter survival. Temperatures below the bark of around −40 °F can cause extensive mortality of overwintering larvae, but the duration of these lethal temperatures needed is not well understood and can vary with time of the year (Wygant 1940, Yuill 1941, Bentz and Mullings 1999, Régnière and Bentz 2007).

How Has MPB Affected Colorado Forests?

Recent MPB outbreaks in North America have been severe in mortality levels and extent, occurring from the southern Rockies to British Columbia. Studies have been conducted across this range addressing many MPB-related topics. Here, we focus on studies conducted in Colorado, particularly in lodgepole pine forests. Studies conducted and observations made here help tell the story of changing forests in Colorado associated with MPB.

Management and Policy Implications

The recent MPB outbreak in Colorado has affected numerous ecosystem services provided by forests. We are only beginning to understand how this large-scale MPB epidemic has changed and continues to influence biological, physical, and societal facets of our forests. Recent and continuing research is moving toward a better understanding of how ecosystem services are being affected and continue telling the story of MPB in Colorado.

Stand Structure and Tree Mortality

During the early stages of the outbreak, MPB attacked stands with higher lodgepole pine basal area (Klutsch et al. 2009). Stands dominated by lodgepole pine in north central Colorado vary from drier to moister sites and from pure lodgepole pine to lodgepole pine mixed with spruce (*Picea Engelmanii*), fir (*Abies lasiocarpa*), and/or aspen (*Populus tremuloides*). MPB mortality reduced lodgepole pine tree density and basal area by 62 percent and 71 percent in infested stands, respectively, and lowered the mean diameter of live lodgepole pine by 53 percent in infested stands (Klutsch et al. 2009). The number of live lodgepole pine trees > 5.0 inches declined over 50 percent between 2002 and 2012, while the number of small diameter trees remained unchanged (Thompson et al. 2017). Over the next century, lodgepole pine is expected to dominate harvested stands, while untreated beetle-killed stands will likely see increased age and species diversity with subalpine fir dominating many sites and increased aspen where present (Collins et al. 2011). Diskin et al. (2011) surveyed affected lodgepole pine–dominated stands in Rocky Mountain National Park as the epidemic waned on the western side of the park. They found lodgepole pine remained dominant on 85 percent of the landscape, and there were only moderate increases in the relative abundance of Engelmann spruce, subalpine fir, and aspen. These species became dominant because of lodgepole pine mortality on only a small percent of the landscape. Future species dominance of MPB-affected stands will depend on what is currently present on the site, any management operations, and geographic features, among other factors.

Fiber Resources

Historically, Colorado has not been a large producer of fiber products. Nevertheless, Colorado is experiencing changes in wood production and utilization as the MPB outbreak has encouraged efforts to produce diverse markets. Forests suitable for wood production comprise 11 million acres, nearly half of all Colorado forestlands; 79 percent of these are privately owned (Colorado State Forest Service 2011). In recent years, many mills have closed and the forest industry infrastructure is limited. From 2002 through 2012, wood products facilities declined from 133 to 58 (Thompson et al. 2017). The Peak to Peak Wood program is a consortium of five Front Range counties cooperating to develop markets as fuel reduction treatments become a consistent source of fiber. Individuals and small businesses have marketed specialty blue-stained wood products from MPB-killed trees. Beetle-killed trees provide material for pellet mills in Walden and Kremmling that produce heating pellets, pet bedding, garden products including wood chips and potting soil, and absorbents used in cleaning spills associated with oil and gas drilling (Confluence Energy, http://www.confluenceenergy.com, last accessed April 2018). A company in Steamboat Springs has developed an innovative wood-strand material suitable for mitigating air and water-caused erosion in burned area stabilization efforts, road maintenance and obliteration, mine reclamation, construction, and other disturbed soil projects (Wood Strand Erosion Control Mulch by Forest Concepts, http://www.woodstraw.com, last accessed April 2018). Various local biomass plants increased consumption of beetle-killed trees. The largest biomass plant in the state, located in Gypsum, burns wood to generate 11.5 megawatts of electricity per hour—enough to power 12,000 homes served by Holy Cross Energy (Eagle Valley Clean Energy, http://www.evergreencleanenergy.com, last accessed April 2018). Studies examining ethanol production from MPB-killed trees from Colorado have demonstrated that trees dead for about a decade are still good for efficient ethanol production (Zhu et al. 2011).

Water Yields, Water Quality, and Biogeochemistry

Watersheds in the Rockies provide water for about 60 million people. Beetle-killed trees may alter water yields and quality (McCray et al. 2014). Edburg et al. (2012) presented a chronological model of cascading ecosystem impacts over the course of and following an MPB epidemic that may help prioritize future research related to post-epidemic changes to water yields and biogeochemistry with and without forest management. The removal of canopy cover through timber harvest increases water yield as a result of reductions of snow interception and transpiration (Stednick and Troendle 2016). The question then follows whether beetle-caused tree mortality would manifest akin. How hydrological processes are affected by disturbances such as MPB is difficult to study and is influenced by many factors such as mortality levels that reduce transpiration, changing canopy structures that reduce interception, and increased solar radiation, which augments evaporation. The interaction among these processes and inherent watershed attributes will make predicting beetle effects difficult (Mikkelson et al. 2013a). In essence, extensive levels of MPB-caused tree mortality can be considered a "forest die-off" where canopy loss, although not continuous across the landscape, results in a reduction of transpiration and canopy interception (Adams et al. 2012).

A number of studies have been published on water flows and yields after beetle-caused tree mortality with variable results. Bethlahmy (1974, 1975) examined water yields in Colorado following an extensive spruce beetle (*Dendroctonus rufipennis*) eruption in the 1940s that killed about 80 percent of the spruce trees in central Colorado and reported a 10 percent increase in water yield, albeit during wet years. During the five years following an MPB outbreak in lodgepole pine in Montana that caused about 35 percent tree mortality, Potts (1984) reported a 15 percent increase in annual water yield, with snowmelt occurring two to three weeks earlier. Some studies examined the impact of MPB-caused tree mortality on snow accumulation and melt in Colorado and indicated that the loss of needles and canopy results in reduced interception, snow accumulation increases, and higher radiation levels reaching the snowpack, causing faster snowmelt and increased water yields (Pugh and Gordon 2012, Pugh and Small 2012, Mikkelson et al. 2013b). Bearup et al. (2014b), working in Rocky Mountain National Park, indicated a 30 percent increase in groundwater attributed to reduced transpiration by killed trees. In contrast, Slinski et al. (2016) compared water flows in watersheds across the West and indicated no changes in postoutbreak flows compared with pre-outbreak. The loss in transpiration from killed trees may be offset by water utilization by ecosystem responses such as understory release. Wehner and Stednick (2017) also indicated that groundwater increased with increasing basal area killed; however, when factors such as decreased snow accumulation and rainfall are considered, annual water yields may not be affected.

MPB effects on water quality and biogeochemistry have received less attention. Rhoades et al. (2012) examined nitrate concentrations in streamflows and indicated no increase associated with beetle-caused tree mortality. Instead, uptake by residual live vegetation and unaffected soils allow retention of nitrates. The growing understory slows runoff and nutrient input into waterways. Clow et al. (2011) sampled soils under live and killed trees and collected water samples from streams. They indicated that soil moisture and soil nitrogen increased beneath killed trees, perhaps because of reduced evapotranspiration, litter accumulation, and decay. Consistent with the findings of Rhoades et al. (2012), no changes were observed in stream water nitrate or dissolved organic carbon. Clow et al. (2011) also reported an increase in total nitrogen and total phosphorus, possibly because of litter breakdown or increased productivity related to warming air temperatures. Cigan (2015) found increased nutrients in the organic soil layer from needle litter and decreased mineral soil phenols and root mass over four years following mortality. Bearup et al. (2014a) examined content and mobility of various metals in areas affected by MPB and observed differential movement of various metals. Brouillard et al. (2016) indicated increases in total organic count levels at water treatment facilities were influenced by MPB-caused tree mortality. Moore et al. (2013) working with MPB in north central Colorado and Reed et al. (2014) and Frank et al. (2014) working with MPB and spruce beetle at sites in Wyoming just north of the Colorado border used eddy covariance and tree measurements to examine the influence of bark beetle–caused tree mortality in photosynthesis, respiration, and water and carbon fluxes. Although tree mortality had influence on these processes, other ecosystem interactions such as the establishment of new understory vegetation and resource utilization by surviving trees were also key. In sum, changes in biogeochemistry influenced by bark beetles are not extensive but are also dependent on specific processes, mortality levels, and forest structure and may change over time.

Wildlife Habitat

Little information is available on how the MPB-caused tree mortality has affected wildlife. Sensitive species in Colorado include flammulated owls (*Psiloscops flammeolus*), boreal owls (*Aegolius funereus*), pine squirrels (*Tamiasciurus hudsonicus*), northern goshawks (*Accipiter gentilis*), boreal toads (*Bufo boreasboreas*), American marten (*Martes americana*), olive-sided flycatchers (*Contupus cooperi*), and the snowshoe hare (*Lepus americanus*). Corridors for the recently reintroduced threatened species Canada lynx (*Lynx canadensis*) may be affected. While the habitats of some species are negatively affected by MPB epidemics, others are positively influenced. A review by Saab et al. (2014) indicated positive responses to MPB mortality by birds such as cavity nesters, shrub nesters, and bark-drillers, while mammals' responses were mixed. Studies consistently reported negative associations by red squirrels dependent on conifer seeds. MPB effects on other understory small mammals may be modulated by postepidemic production of grass, forb, and shrub species and accumulation of coarse woody debris. Northern goshawks are more influenced by the availability of prey and open understories that facilitate flight than by forest type. In the short term, when prey is still available, goshawks will likely maintain their territories. When the overstory is no longer present and prey populations decline, they may shift territories; however, as the forest recovers, populations and territory occupation will likely return to pre-MPB outbreaks levels. In riparian areas, MPB removes the larger trees, reducing canopy cover over streams, increasing water temperatures and woody debris levels and changing riparian vegetation. Increased water temperature could reduce cold water fish habitat in lower elevations areas and areas adjacent to meadows where temperatures may already be elevated. On colder high elevation sites, habitat for some fish species could be enhanced with warmer temperatures. Large woody debris in the streams could improve cover and possibly create pool habitat for fish and amphibians. Increased riparian woody and herbaceous plants may provide food for wildlife, nesting habitat for songbirds, and increased insect diversity.

Fire and Bark Beetle Interactions

Fire and bark beetle interactions take two principal forms. First, nonlethal fire injury can make trees susceptible to insect attack which can cause trees that may have survived the fire to die. This has been the case following recent fires in Colorado, yet few studies have addressed this. The 2000 Bobcat Gulch Fire in northern Colorado occurred in a ponderosa pine forest, and Sieg et al. (2006) indicated that crown scorch and consumption were the best predictors of tree mortality to fire. Negrón et al. (2016) working in the same area indicated that the most common insects attacking fire-injured trees were Ips beetles (*Ips pini*), red turpentine beetle (*Dendroctonus valens*), and various woodborer species. Attacks were associated primarily with bole scorch and tree diameter. The same species are likely the most frequent in postfire lodgepole pine forests.

The second form of fire and bark beetle interactions considers whether bark beetle–caused tree mortality increases the likelihood of fire occurrence or affects fire behavior or both. As beetle-killed trees die, live fuels are transformed. In northern Colorado, lodgepole pine needles become more flammable after tree mortality as they dry (Jolly et al. 2012). An increase in downed fuels occurs, particularly in the large classes as dead trees fall. For example, Klutsch et al. (2009) reported increased litter layer depth and height of herbaceous vegetation postoutbreak and projected a four-fold increase in coarse woody debris by the time 80 percent of the dead trees fall to the ground.

Studies have used field data and fire models to predict potential fire behavior. Results vary among studies, in part, because different models are based on different processes and assumptions, types of data used by specific models, phase of the outbreak or time since outbreak when data were collected, and fire conditions and parameters used for model runs. For example, Klutsch et al. (2011) and Simard et al. (2011) indicated that under extreme fire conditions, uninfested stands exhibited and sustained more crown fires than infested stands. In contrast, Page and Jenkins (2007) indicated that crown fires were more likely in postepidemic stands. Schoennagel et al. (2012) indicated that the likelihood of an active crown fire was higher in beetle-affected stands, but such fires in lodgepole pine forests usually occur during dry and extreme weather conditions. A key relevant concern with fire behavior in beetle-affected areas is the difficulty in controlling fires and firefighter safety (Schoennagel et al. 2012, Jenkins et al. 2014). Fire behavior in beetle-killed stands will be determined by local conditions such as weather conditions, terrain, time since tree mortality, and forest composition, making overarching statements difficult.

Another important question is whether beetle-caused tree mortality can increase the likelihood of fire occurrence. Limited work in lodgepole pine in Colorado suggests that this may not be the case. West (2010) sampled 57 burns in the Arapaho-Roosevelt and the White River National Forests, searching for locations where MPB-caused tree mortality had occurred in the 1980s. Evidence of MPB was found in only two burns. A spatial analysis of 466 fires (all but one less than an acre) from 1980 to 2005 did not find a relationship between MPB-caused mortality and subsequent fires. Kulakowski and Jarvis (2011) examined burned and unburned lodgepole pine stands and indicated that beetle-caused mortality did not increase fire probability. Observed fires were driven by climatic factors that foster dry conditions, which is consistent with previous studies (Arno 1980, Buechling and Baker 2004, Sibold and Veblen 2006).

Invasive Species

Invasive plant species are a major threat to native flora and biota diversity. Control programs are difficult and expensive. In Colorado, land use and fragmentation associated with population growth and tourism have created environments suitable for the establishment of invasive species (Flint et al. 2012). Tree mortality caused by MPB creates openings where understory vegetation can become abundant and invasive plants have the possibility of outcompeting native vegetation if present or where sites are disturbed by logging. However, we did not find studies documenting the establishment of invasive species in MPB-affected forests nor invasive species outcompeting native species in these sites. Daab and Flint (2010) conducted surveys through questionnaires sent to residents in the counties most affected by MPB in northern Colorado. In general, residents were aware of the consequences of invasive species but were unfamiliar with local species. Residents, although willing to take action, were not doing so perhaps because of costs and time concerns.

Human Dimensions

MPB in the Urban Environment and Hazard Trees

This recent MPB outbreak in Colorado also killed trees in the urban environment. In mountain towns, communities, cities, towns, and shelterbelts on the plains in eastern Colorado as far as Yuma, trees were attacked by MPB. In Fort Collins, 232 trees were killed by MPB between 2008 and 2013, mostly Scots pines (*Pinus sylvestris*). Removal of a tree killed by MPB costs about $700 (Zentz 2017, pers. commun.).

The Rocky Mountain Region of the Forest Service has made human safety a priority. Hazard trees affected about 3,700 miles of roads, 460 recreation sites, 16 ski areas, and about 560 miles of power lines. About 1,200 miles of hiking trails have been affected by beetle-killed trees (Figure 1). Ambitious hazard tree removals have been implemented in many locations. In northern Colorado in 2010, hazard tree removal was conducted along about 275 miles of roads, 162 miles of trails, and at 210 recreation sites; 13,000 acres were treated for fuel reduction at a total cost of $32 million (USFS Region 2 2011). An interesting approach was implemented in 2011, in an area in the White River NF which was too steep for machinery or chainsaws. The Eagle/Holy Cross Ranger District felled 661 hazard trees by blasting them with explosives (USFS Region 2 2011).

Residential Property, Public, and Spiritual Values

MPB-caused tree mortality reduces the satisfaction from ecosystem goods and services, particularly the value of forest amenities (Price et al. 2010). In an analysis of how MPB-killed trees impact property values in the wildland-urban interface in Grand County, Price et al. (2010), indicated that property values are reduced by $648, $43, and $17 for every MPB-killed tree within a 0.06, 0.3, and 0.6 mile buffer, respectively.

Many factors, not well understood, influence how the public and society in general respond to as large a forest disturbance as this MPB outbreak. For example, Kooistra and Hall (2014) indicated that factors such as gender, areas of concern, and even political views will color how people react to the outbreak, and even factors affecting different groups are not consistent. In their surveys, groups that supported some type of management may be more concerned about the impact of the management than the outbreak itself. Views may also change during the course of the outbreak. McGrady et al. (2016) examined personal value orientations and their relationship to the outbreak and forest management. People exhibited four types of value orientations, including a biocentric orientation toward forest features such as ecological, spiritual, and aesthetic values but not based on human needs. Anthropocentric values focused on wise forest management for the betterment of humankind including recreation, an intermediate value orientation or pluralistic value, and lastly a spiritual or therapeutic value. Based on surveys of residents in or near forests in Colorado and Wyoming, they indicated variation of emphasis among values and forest utilization. One-third of the respondents supported control of MPB infestations and wood utilization, while another third preferred letting the forest "take its own course" (McGrady et al. 2006, pp. 191–192, 194). The last third had mixed views. Over half of the respondents had a positive view of how the Forest Service manages forest lands. The spiritual group also had the attitude of letting the forest respond. They find the forest as a place of rest, peace, spirituality, and a sense of "what we are, where we came from, how our ancestors lived" (McGrady et al. 2006, p. 190). A respondent indicated that the forest "brings me closer to God and the universe; it is a constant place of rejuvenation and enjoyment" (McGrady et al. |2006, p. 190).

The spiritual values of forests are not well understood, but some studies provide insights. Kauffman et al. (1992) indicated that an important value of old-growth forests is the cultural and spiritual heritage, with the presence of large trees accompanied by the absence of human disturbance being critical factors. Clement and Cheng (2011) conducted social surveys across three National Forests in Colorado and Wyoming. When a random sample of participants were asked whether they, "value these Forests because they are a sacred, religious, or a spiritually special place to me or because I feel reverence and respect for nature there" (Clement and Cheng 2011, p. 396), 33 percent of the respondents across forests indicated that this was a relevant value. Interestingly, most of the respondents were in favor of the removal of infested trees, as long as it was not for commercial purposes. Although spiritual and cultural values are affected by mortality of large trees by MPB, the impact of the large extent of the recent mortality on peoples' values is still not well understood. Morris et al. (2018) indicated a need for better ways to examine the highly complex and for multifaceted responses to outbreaks.

In syntheses on the human reactions to insect outbreaks, Flint et al. (2009, 2012) indicated that affected communities in parts of Colorado range from upscale resorts to rural communities. Across groups, major concerns about the MPB epidemic included loss of aesthetics, the high cost of mitigation, effects on recreation and tourism, and potential or perceived fire hazard. Regarding salvage of dead trees, attitudes were less supportive in tourism-supported areas, but forest industry activities were supported in areas with existing and historical resource utilization.

Recreation and Visual Quality

Hundreds of campgrounds and miles of hiking trails have been affected by MPB and spruce beetle. Dead tree cover has been removed in many developed recreational sites and along roadways. Removal of hazard trees along roads resulted in temporary closures, negating access to popular recreation areas in northern Colorado. Young trees, seedlings, and wildflowers have begun to soften the look of clearcuts in recreation sites. We are not aware of specific studies to determine the impact of the Colorado MPB epidemic on visual quality. Sheppard and Picard (2006) reviewed available literature on this topic and found scenic beauty and visual preference were negatively impacted by MPB outbreaks. However, informed subjects that understood insect infestation expressed a more negative perception than those subjects with no knowledge of the infestation. In Colorado, surveys conducted by Arnberger et al. (2018) indicated that forest condition influenced visitor enjoyment of landscapes. Visitors preferred mature healthy forests compared with stands with tree mortality.

Concluding Remarks

Studies and available information on the recent MPB outbreak in Colorado have produced invaluable information. Research is continuing in many aspects but particularly important gaps in information exist in some areas such as the effects on wildlife, the response of invasive species, ways to measure nontimber impacts, and clarification of sometimes variable findings regarding water yields and fire and beetle interactions. It is important to realize that answers will not necessarily be the same in all places but will also depend on initial conditions and vary with time. As a result, encompassing statements need to be made and viewed with caution. It is our hope that the collapse of the outbreak does not lead to waning interest but that we continue to learn more as the story of MPB in Colorado continues to unfold.

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