



Reconstructing historical outbreaks of mountain pine beetle in lodgepole pine forests in the Colorado Front Range

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ABSTRACT

Regional-scale mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the first decade of the 2000s affected millions of hectares of lodgepole pine (*Pinus contorta*) in western North American forests. In Colorado, 1.4 million ha exhibited high mortality. These events prompted questions about whether historical outbreaks reached the scale of this most recent event. We aimed to reconstruct past mortality events in lodgepole pine forests in the northern Colorado Front Range and to determine whether these were of similar extent to the 2000s outbreak. We identified logs of mountain pine beetle-killed trees based on visually identifiable signs of beetle infestation including lower bole breakage, egg galleries, exit holes, and the presence of blue stain. We collected cross-sections, developed tree ring chronologies and determined death dates through tree ring analysis. We detected five mortality events since the 1860s, including widely distributed mortality in the 1910s that was geographically as extensive as the 2000s outbreak in our study area. Trees killed were on average 232 years of age and 36 cm in diameter. In our study area, it takes about 200 years for a lodgepole pine to reach the size suitable for mountain pine beetle attack. We conclude that mountain pine beetle infestation signs remain useful for identifying mountain pine beetle-caused tree mortality for over a century and that well-distributed mountain pine beetle-caused mortality has occurred in the past in the northern Colorado Front Range. Future reconstructions of bark beetle-caused mortality may benefit from integrating the use of beetle symptomatology with growth releases. The inclusion of stand demography and fire history will present a holistic picture of how disturbance interactions create the mosaic of forest landscapes. Awareness of the disturbance histories in forests and the legacies of past events advances understanding of their ecology and will inform researchers and managers in developing management strategies to foster sustainable delivery of ecosystem services and maintain resiliency as climate change manifests.

1. Introduction

During the first two decades of the 21st century, large episodes of extensive tree mortality caused by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins; Coleoptera: Curculionidae: Scolytinae; MPB hereafter) have occurred in western North America, mostly in lodgepole pine (*Pinus contorta* Dougl. Ex. Loud.) forests and extending from the Southern Rocky Mountains to British Columbia in Canada (Hrinkevich and Lewis, 2011; Jarvis and Kulakowski, 2015; Negrón and Fettig, 2014). In Colorado, about 1.4 million hectares were affected by MPB from 1996 to 2013 (referred to as “2000s outbreak” hereafter). Annual mortality reached its highest levels in 2008, after which populations declined (Harris, 2014). Stand mortality levels across the landscape ranged from little or no mortality to almost complete mortality. On average, about 62% of the basal area and about

71% of trees were killed in lodgepole pine forests in north-central Colorado (Klutsch et al., 2009). Given the large geographical distribution (extent) and high tree mortality levels (intensity) observed during the 2000s outbreak, land managers, the public, and policy makers question whether this outbreak exceeded past mortality events in extent or intensity, or both, motivating the need to study and better understand the history of MPB-caused tree mortality.

Forests are constantly influenced by disturbances at various spatial and temporal scales that shape their composition and structure (Oliver and Larson, 1996; White and Pickett, 1985). Natural disturbances can be abiotic, such as wind storms, fires, and avalanches, or biotic agents such as disease-causing pathogens or forest insects (Castello et al., 1995; Foster et al., 2018; Temperli et al., 2013). Historical patterns of fire are likely the most studied disturbance regimes in the American West (Kipfmüller and Baker, 2000; Sibold et al., 2006; Sibold and

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Veblen, 2006; Swetnam and Baisan, 1996; Swetnam and Betancourt, 1998), but pathogens and insects are significant shapers of forests and interact with other disturbances (Castello et al., 1995; Negrón et al., 2014; Swetnam and Lynch, 1993). Forested areas affected by bark beetles can be as extensive as those affected by fire (Hicke et al., 2006).

Lodgepole pine is one of the most widely distributed tree species in North America, ranging from the Yukon peninsula in western Canada south to Baja California and the southern Rocky Mountains in Utah and Colorado (Critchfield and Little, 1966; Lotan and Critchfield, 1990). Lodgepole pine forests can be composed of single or multiple age cohorts and may grow in pure or in mixed stands. In Colorado, lodgepole pine forests cover about 690 k hectares, comprising about 7% of the forested area (Colorado State Forest Service, 2012). Lodgepole pine forests commonly establish after stand replacing or mixed-severity fires (Aoki et al., 2011; Arno, 1980; Kipfmüller and Baker, 2000; Schoennagel et al., 2003). Stands with serotinous cones tend to produce single cohort stands following fires; subsequent disturbances open the canopy to allow younger trees to establish, creating multiple cohort stands (Peet 1981, Sibold et al., 2007).

The MPB is one of the few species of bark beetles that cause spatially extensive tree mortality in forests. Its geographical distribution extends from British Columbia south to Baja California, Arizona, and New Mexico and east to the Black Hills of South Dakota (Wood, 1982) and Nebraska (Costello and Schaupp, 2011). Its range is now expanding to the north in British Columbia and east into Alberta as a result of climate change (Cullingham et al., 2011; de la Giroday et al., 2012; Hrinkevich and Lewis, 2011). About 15 species of pines (*Pinus* sp.) are known to be hosts (Negrón and Fettig, 2014), with lodgepole pine being one of the most frequently infested, widely distributed, and abundant. Mountain pine beetle is always present in forests in low-level populations that infest stressed or injured trees and trees infected by pathogens such as root disease or mistletoe infections (Klutsch et al., 2014; Schmid and Mata, 1996).

Bark beetles are key components of forest ecosystems. Endemic populations kill single trees or small groups of trees, resulting in small-scale canopy gaps that characterize healthy, functioning ecosystems (Lundquist and Negrón, 2000; Sibold et al., 2007). Epidemic populations result in spatially extensive tree mortality (Chapman et al. 2012; Harris, 2014; Negrón and Fettig, 2014; Raffa et al., 2008; Schmid and Mata, 1996). Both endemic and epidemic populations shape forest structure and composition at different spatial and temporal scales. Infested trees provide food for foraging woodpeckers and snags provide habitat for avian species (Saab et al., 2014). Dead trees eventually fall at a rate influenced by tree size, stand conditions, and weather (Mitchell and Preisler, 1998), opening the canopy and fostering the establishment of trees and understory vegetation, as well as creating woody debris that provides habitat for ground-dwelling wildlife and a large community of invertebrates and fungi that contribute to decomposition and return nutrients to the soil (Harmon et al., 1986).

Mountain pine beetles prefer large-diameter trees (> 20 cm) growing in dense stands as large trees have thick phloem that provides ample food for insects to develop and increase populations (Amman, 1972). Dense stands provide abundant hosts and are more likely to be infested, exacerbating tree mortality levels (Safarynik et al., 1974; Amman et al., 1977; Negrón and Klutsch, 2017). Climatic conditions influence bark beetle populations (Chapman et al., 2012; Hicke et al., 2006) as increased temperatures can provide thermal conditions favorable for population development (Powell and Logan, 2005) and warmer winter temperatures can increase survival of overwintering populations (Bentz et al., 2010). Drought conditions stress trees and compromise their defensive mechanisms (Berg et al., 2006; Franceschi et al., 2005; Kolb et al. 2016; Mattson and Haack, 1987), facilitating successful beetle infestation and reproduction. The frequency and duration of outbreaks are variable and influenced by factors such as weather conditions that may negatively affect insect populations or enhance tree resistance, or both. The return interval of bark beetle

epidemics is determined by climate, the time needed for surviving or regenerating trees in a previously affected stand to grow and become susceptible hosts anew, and the abundance of large diameter trees surviving a previous outbreak (Jarvis and Kulakowski, 2015; Schmid and Frye, 1977). Disturbance regimes of fires and bark beetle outbreaks are both expected to become more frequent and intense under climate change (Bentz et al., 2010; Schoennagel et al., 2017; Seidl et al. 2017).

To better understand how disturbance processes and their effects operated historically, we must rely on the interpretation of processes through reconstructed ecological history using proxy data such as tree rings (Axelson et al., 2009). One of the effects of beetle-caused tree mortality is the increase in resources for surviving trees that can result in increased growth. This response can be used to identify previous bark beetle outbreaks by detecting growth releases in annual rings of surviving trees (Roe and Amman, 1970). Various studies have advanced this idea, resulting in successful approaches for reconstructing past outbreaks of the spruce beetle (*Dendroctonus rufipennis*) (Berg et al., 2006; Veblen et al., 1991) and MPB (Axelson et al., 2009, 2010; Campbell et al., 2007; Jarvis and Kulakowski, 2015; Heath and Alfaro, 1990). Recorded and reconstructed histories of MPB outbreaks in lodgepole pine forests outside the Colorado Front Range (CFR, hereafter) report dates as far back as 1785, but most are more recent, including the periods of 1870–1890, around 1916, and 1924 in Utah (Roe and Amman, 1970; Thorne, 1935). In British Columbia, examination of historical MPB outbreaks have recorded from 3 to 5 episodes of varying intensities since the 1890s (Axelson et al., 2009, 2010; Hawkes et al., 2004). In Colorado, several studies have provided partial reconstructions (Kulakowski et al., 2012; Kulakowski and Jarvis, 2011) of MPB outbreaks and a comprehensive reconstruction from the 1700s through 2000s on the western slope of the Continental Divide (Jarvis and Kulakowski, 2015). These studies demonstrate how the use of dendrochronological cross-dating of growth releases has been a successful approach for reconstructing historical bark beetle outbreaks. However, growth releases can also result from other disturbances that cause tree mortality in a stand, such as blowdowns and mixed severity fires or favorable weather conditions (Alfaro et al., 2004; Eisenhart and Veblen, 2000; Veblen et al., 1991), therefore inferences must be framed considering disturbance interactions.

Another approach that could be useful for examining historical MPB outbreaks may be reconstructing the death dates from remnant logs of beetle-killed trees. When the insect kills trees, characteristic signs remain in the logs that can be identified many decades after the tree has died. These signs are the product of the MPB life cycle. We tested this approach to identify episodes of MPB-caused mortality.

Our study area is located in the northern CFR, east of the Continental Divide. Forests differ from those on the west side of the Continental Divide because of drier conditions and fires generally being more frequent and less extensive in the CFR compared to the western slope (Sibold et al., 2006; Sibold and Veblen, 2006). These factors may be responsible for different outbreak dynamics and regimes in the CFR than those documented elsewhere. While some written records exist from the mid- to late 20th century, the historical regime of outbreaks in the CFR is largely unknown. In this study, we set out to reconstruct the history of MPB outbreaks on the east slope of the Rockies in northern Colorado using dendrochronological methods. We asked and were able to answer the following questions: Can we rely on insect signs remaining on downed logs to identify victims of past MPB mortality? Can we use death dates from these logs to reconstruct outbreaks? What is the history of MPB outbreaks in lodgepole pine forests in the northern CFR?

2. Methods

2.1. Study area

The study was conducted during the summers of 2012, 2013, and

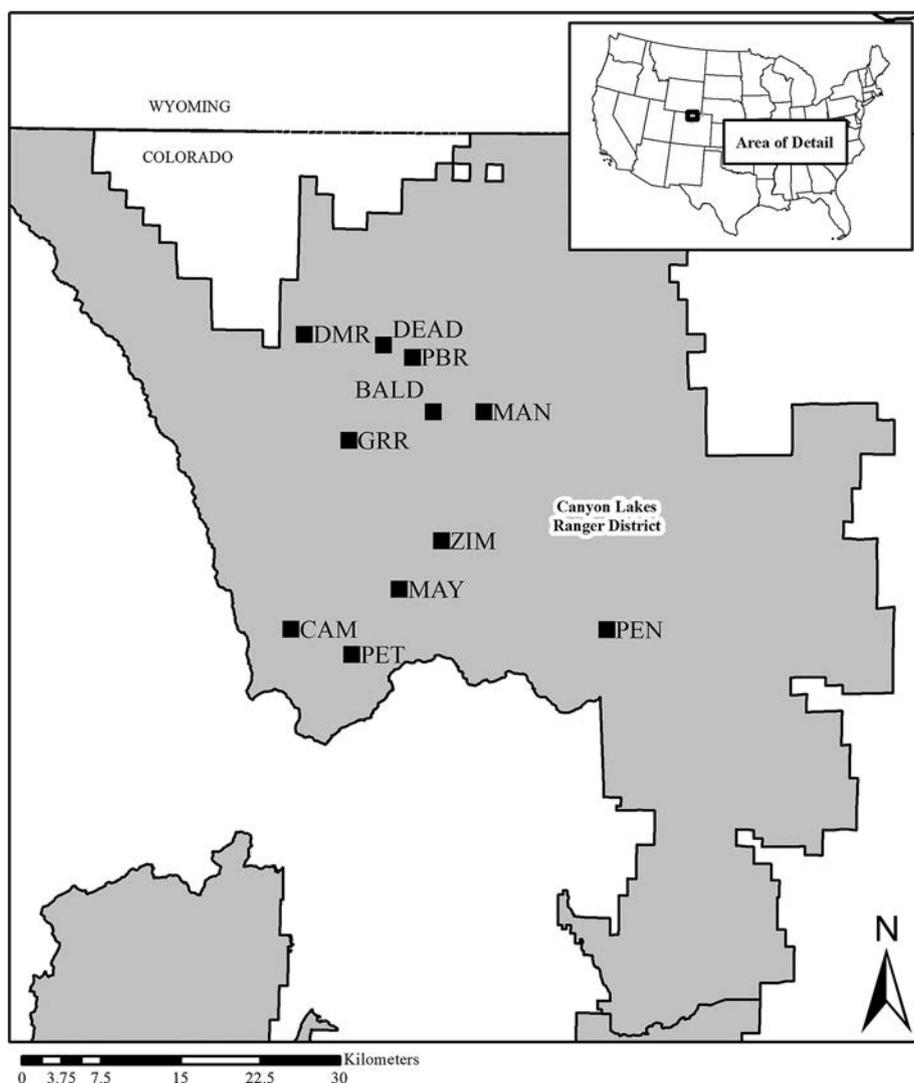


Fig. 1. Study site locations within the Canyon Lakes Ranger District of the Arapaho-Roosevelt National Forest in northern Colorado. Study sites are identified by letter codes; see Table 1. The PEN site is located about 34 km directly west of the city of Fort Collins and the PET site is located about 5 km north of the Arapaho-Roosevelt National Forest boundary with Rocky Mountain National Park.

2015 on the Canyon Lakes Ranger District of the Arapaho-Roosevelt National Forest in Larimer County, Colorado, USA (Fig. 1). This is the northern part of the CFR, the easternmost range in the Southern Rocky Mountains, which extends from the Laramie and Medicine Bow Mountains in Wyoming and south to the Arkansas River in Colorado (Fenneman, 1931; Whitney, 1983). Forested ecosystems occur from about 1700 m to 3500 m in elevation, with lodgepole pine dominant between 2400 m and 3000 m (Peet, 1981). In the CFR, lodgepole pine occurs in upper montane mixed conifer and subalpine forests. In the upper montane, between 2300 m and 2700 m in elevation, it forms pure stands or grows in mixed stands with ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.), limber pine (*Pinus flexilis* James), aspen (*Populus tremuloides* Michx.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Colorado blue spruce (*Picea pungens* Engelm.), depending on topography, moisture, aspect, and disturbance history. In subalpine forests above 2700 m elevation, lodgepole pine may occur in extensive pure stands, in mixed stands with Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) and limber pine, or may be seral to spruce-fir forests (Peet, 1981).

The center of the study area was located at UTM 13 T 441208, 4,500,166 (NAD27). A polygon around the area connecting the outermost sampling locations has a perimeter of about 94 km and encompasses about 635 km². We used lodgepole pine old-growth (Mehl,

1992) maps produced by the Arapaho-Roosevelt National Forest to identify potential study sites. Using the maps we conducted walk-through surveys and identified 11 sites for sampling that met the following criteria: old-growth structure dominated by lodgepole pine, relatively undisturbed except for signs of past and recent MPB mortality and with only scattered logging, and with a *Pinus contorta* / *Vaccinium scoparium* plant association (Hess and Alexander, 1986; Johnston, 1987). This vegetation type occurs primarily on gentle slopes and ridges in both subalpine and upper montane forests dominated by lodgepole pine; therefore, our study area is typical of lodgepole pine stands in the northern CFR. The climate is cool and dry and near the centroid of the study area, at 3000 m in elevation, 30-year (from 1981 to 2010) normal mean temperature in January is -5°C , mean July temperature of 15°C , and yearly precipitation is 425 mm (PRISM Climate Group, <http://prism.oregonstate.edu/> (Accessed May 2019).

We wanted to determine if the areas with mortality from the 2000s outbreak had been affected in the past; therefore, we deliberately selected sites that had mortality from this most recent outbreak. Study sites were characterized by areas of similar topography, and varied in size from 3.5 to 85 ha, averaging 27 ha (Table 1). Sites ranged in elevation from 2801 m in lodgepole pine-dominated mixed conifer forest, to 3261 m in lodgepole pine-dominated subalpine forest, with a mean elevation of just above 3000 m, encompassing the range of elevation of

Table 1
Site names with identification codes and topographic data for study sites. Sites are listed from north to south.

Site name	Site code	Elevation (m)	Slope (%)	Area (ha)	Aspect
Pearl Beaver Road	PBR	3002	10	3.5	SE
Deadman	DEAD	3210	10	12.2	S
Deadman Road	DMR	3100	15	23.0	SE-W
Bald Mountain	BALD	3261	10	75	S
Manhattan	MAN	2845	15	85.0	SE
Green Ridge Road	GRR	3081	5	33.0	S
Zimmerman	ZIM	3232	20	2.2	E
May Creek	MAY	3251	12	8.9	N
Pennock Pass	PEN	2801	15	3.5	NE
Cameron Pass	CAM	2965	20	3.3	S
Petersen Lake	PET	2978	15	52.1	NE
Mean (se)		3066 (49)	13.4 (1.4)	27.4 (9.1)	

lodgepole pine-dominated stands in the area. All sites were located on slopes less than 20% and included all aspects, though southerly and easterly aspects were most frequent.

2.2. Field methods

We selected logs for sampling based on a set of criteria developed to ensure that they had been killed by MPB (MPB-killed logs hereafter) prior to the 2000s outbreak. Criteria for older MPB-killed logs included gallery scoring on the wood surface (Fig. 2), the presence of remnants of outer bark on some part of the log surface that would allow identification of MPB galleries in the underside of bark remnants (Fig. 3) and exit holes (Fig. 4), presence of blue stain fungi in the sapwood (Fig. 5), and stem breakage in the lower bole above the roots (Fig. 6). The presence of bark on some part of the wood surface allowed determination that the date of the outermost ring was the death date of the tree. If no bark was attached to the sample, but bark was intact elsewhere on the logs we knew the outermost ring on the sample was close to the death date, off by only a few years due to possible erosion of outer



Fig. 2. Mountain pine beetle egg gallery and larval galleries, perpendicular to the egg gallery, scoring the wood surface of a lodgepole pine. These were often exposed or visible once a section of bark was removed.



Fig. 3. Mountain pine beetle egg gallery and larval galleries on the inside surface of a section of bark removed from a mountain pine beetle-killed log. These were easily observed on bark removed from logs or found under them.



Fig. 4. Mountain pine beetle emergence hole on bark surface collected from a mountain pine beetle-killed log. Emergence holes are readily observed and upon removal of a section of bark, egg galleries can be found. The emergence holes are rounded and about 2 mm in diameter.



Fig. 5. Blue-stained sapwood in a stump from a mountain pine beetle-killed tree. Upon entering the tree, mountain pine beetle introduce symbiotic fungi that grow into the ray parenchyma cells of the wood causing a characteristic blue coloration of the sapwood called “blue stain”. The fungi can only establish in the fresh sapwood when the tree is killed and persists after tree death. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rings.

We determined these selection criteria based on the MPB life cycle. Mountain pine beetle usually exhibits one generation per year, and its dispersal flight in Colorado occurs in late July-early August when adults emerge from trees attacked the previous year (McCambridge, 1964; Tishmack et al., 2005). Using a complex chemical communication



Fig. 6. Mountain pine beetle-killed tree broken at lower bole. Trees killed by mountain pine commonly break low on the trunk at about 0.6 m, though we observed tree breakage of killed trees up to about 3 m. This is because after tree death, the base and lower bole of beetle-killed trees maintain a level of moisture adequate for the development of wood-rotting fungi and the resulting bole decay leads to stem breakage. Less commonly, trees may tip over with root masses and soil attached.

system of pheromones and host chemicals, gustatory and visual cues, and random landings (Campbell and Borden, 2006; Hynum and Berryman, 1980; Pureswaran and Borden, 2005; Raffa, 2001; Raffa and Berryman, 1982, 1983; Raffa et al., 2005), beetles attack new trees synchronously in large numbers, overwhelming the primary defensive mechanism of the tree, its resin production system (Franceschi et al., 2005). After successful entry, beetles construct an egg gallery and lay eggs under the bark, lightly scoring the surface of the wood. The insect's egg galleries are distinctively J-shaped: a short bend at its beginning where the beetles entered the tree, then straight, elongated, oriented vertically on the tree trunk and packed with frass produced by the beetles. Galleries scoring the wood persist after the tree has died, even after the bark sloughs off, and, as determined in this study are visible after over a century. Remnants of galleries can also be seen in residual pieces of bark either attached to the tree or found under the log. Over time, yellow resinous streaks become visible on the wood surface that correspond to places where bark sections with galleries were attached. After hatching, larvae develop through the summer, overwinter, and pupate and transform into adults in the spring, completing their life cycle. Adults manducate an exit hole through the bark (Reid, 1962), which is characteristic in size and shape. Upon entering the tree, MPBs introduce symbiotic fungi primarily in the order Ophiostomatales that grow into the ray parenchyma cells of the wood causing a characteristic blue coloration of the sapwood called "blue stain" that persists after tree death (Fig. 5) (Mercado and Ortiz-Santana, 2018; Robinson-Jeffrey and Davidson, 1968; Rumbold, 1941). Common species of fungi causing blue stain include *Ophiostoma montium*, *Grosmannia clavigera*, and *Lep-tographium longiclavatum* (Tsui et al., 2014). These fungi develop in fresh sapwood and cannot develop after the tree dies and the sapwood dries. When blue stain is seen along with other signs of beetle infestation, introduction of the blue stain fungi by MPB can be inferred [Thomas Harrington, personal communication]. Trees killed by MPB tend to break low on the trunk at about 0.6 m (Mitchell and Preisler, 1998; Schmid et al., 1985) although we observed tree breakage of killed trees up to about 3 m. This is because after tree death, the base and lower bole of beetle-killed trees maintain a level of moisture adequate for the development of wood-rotting fungi and the resulting bole decay leads to stem breakage (Lewis and Thompson, 2011; Mitchell and Preisler, 1998). Less commonly, they can tip over with root masses and soil attached, but this is more common as a result of blowdowns or trees

dead for other reasons such as root disease. Mountain pine beetle-killed logs exhibiting these beetle-caused signs can persist for over a century, as noted in this study, particularly in cold dry environments (Brown et al., 1998), allowing identification of beetle-killed trees over a century after tree death, the dates of which can then be determined through cross-dating tree rings.

To select logs for sampling we cruised the study sites and as we encountered downed trees exhibiting stem breakage in the lower bole (< 3 m above the ground; a few were blowdown), we examined them for other signs of MPB infestation. Logs had to exhibit all signs of infestation. Decomposition rates of killed trees varied with factors such as ground contact, sun exposure, and microclimate. As estimating time since mortality is not possible visually, we sampled trees with different levels of degradation, to assure that samples covered as wide a range as possible of time since mortality. For example, the crown of sampled logs varied from still having small to medium-sized twigs to having only large branches or none at all.

Using a chainsaw, we collected cross-sections from logs determined to have been killed by MPB regardless of dbh (diameter at 1.4 m above the ground). Most logs were at least partially suspended above the ground, supported by branches, stumps, or other logs, helping to preserve samples for tree ring analysis. We cut sections as low as possible on the stem and sometimes from the stump to obtain a pith date closest to the actual germination date, but this was not always feasible when wood was rotten. In those cases, sections were taken higher on the stem where outside wood was intact to allow detection of a death date. For each MPB-killed log, we recorded dbh. Sometimes we had to estimate dbh location due to log breakage and accessibility; this measurement could not be adequately obtained from some logs.

Across all sites, we randomly collected 35 cores at 30 cm above the ground from standing dead trees and six cross-sections from dead downed trees that had been killed in the 2000s event to determine age and death dates. This allowed confirmation of mortality during the recent outbreak and allowed assignment of a midpoint year to the mortality event (further discussed below). These recently killed trees had little to no foliage remaining or only small twigs. Bark may have started to detach and fall off the bole but most was still attached.

2.3. Laboratory methods

Sections and cores were processed and visually crossdated using standard dendrochronological techniques (Speer, 2010; Stokes and Smiley, 1968). Sections and cores were dried, glued to wooden mounts for stability and sanded with progressively finer grits of sandpaper until cell structures were visible. To crossdate our samples, we constructed local ring-width chronologies using skeleton plotting for each site and a composite for the study area. We also used chronologies from nearby areas obtained from the International Tree Ring Data Bank (<https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>) for dating control. When pith was not present on a sample, we used the concentric circle method (Applequist, 1958) to estimate rings to pith if the distance to pith was less than 10 rings; otherwise inside date, the date of the closest ring to the pith, was determined. Lodgepole pine trees become susceptible to MPB when they reach 20 cm in dbh, therefore, we used cores from live trees that were between 20.3 cm and 25.4 cm to determine the age at which lodgepole pine becomes a suitable host for MPB in the CFR.

We used the fire history analysis program "Fire History Analysis and Exploration System" (FHAES) (Version 2.0.2, www.frames.gov/fhaes) (Brewer et al., 2016; Sutherland et al., 2016) to visualize timelines of trees and mortality events at each site. Mortality events were determined when the death dates of a group of sampled logs clustered within a period of nearly consecutive years. We used generalized linear mixed models with a gamma distribution to compare age and tree dbh at time of death by MPB among mortality events across all sites, using mortality event as fixed effect and site within mortality event as

Table 2

Number of crossdated mountain pine beetle-killed logs and the earliest pith date determined from sampled lodgepole pines for each site. Samples were cross-sections except one sample from BALD that was an increment core.

Site	Dated MPB-killed logs	Earliest pith dates in chronologies
PBR	11	1670
DEAD	13	1586
DMR	15	1592
BALD	18	1573
MAN	12	1646
GRR	15	1628
ZIM	11	1728
MAY	14	1524
PEN	13	1671
CAM	16	1632
PET	14	1654
Total samples	152	

random effect. All means reported in tables and text are followed by the standard error (SE).

3. Results

3.1. Tree ring chronologies

The number of confirmed MPB-killed logs crossdated per site ranged from 11 to 17 (Table 2). Earliest chronology dates from sampled lodgepole pines ranged from 1524 at the MAY site to 1728 at the ZIM site, indicating that all sites were at least 287 years old; some were 400–500 years old when sampled. The earliest MPB-caused mortality of lodgepole pine dated to 1868 from the BALD site.

3.2. Historical mountain pine beetle outbreaks

Based on the synchronicity of crossdated death dates of MPB-killed logs, we identified 5 historical periods of beetle-caused tree mortality in addition to the 2000s outbreak. Clusters of death dates centered on the years 1868, 1889, 1910, 1945, 1987, and 2012 (Fig. 7; Fig. A.1). These dates will be used to refer to the MPB mortality events hereafter. The plurality of the MPB-killed logs identified were from the 1910 mortality event while only two logs were detected from the 1868 mortality event; one at GRR and one at BALD (Table 3, Fig. 7; for brevity and conciseness Table 3 does not include the two trees from 1868 but they are presented in Fig. 7). Not all mortality events occurred in all sites: two sites experienced mortality in 1868, eight sites exhibited MPB-caused mortality in 1889; all sites in 1910; six in 1945; and four in 1987. All sites had MPB-caused tree mortality in the 2000s (which was part of site selection). Although the 1889 mortality was well-distributed across the study area, most of the MPB-killed logs identified were from the CAM

Table 3

Number of mountain pine beetle-killed logs killed in each mortality event per site. Samples were cross-sections except the 1987 sample from BALD, which was an increment core.

Site	Mortality Events				
	1868	1889	1910	1945	1987
PBR	0	0	11	0	0
DEAD	0	5	8	0	0
DMR	0	2	13	0	0
BALD	1	1	12	3	1
MAN	0	1	9	2	0
GRR	1	1	9	2	2
ZIM	0	1	3	6	1
MAY	0	0	14	0	0
PEN	0	4	3	5	1
CAM	0	9	7	0	0
PET	0	0	9	5	0
Total	2	24	98	23	5

site (Table 3). The 1868, 1945, and 1987 events were more localized, affecting sites predominantly in the central and southeast part of the study area (Fig. 8). Sites PBR, DEAD, and DMR, which were among northern-most sites, and MAY and CAM, which were close to one another, did not record either the 1868, 1945 or the 1987 mortality events. The PBR and MAY sites recorded only the 1910 event in addition to the 2012 event. The GRR, ZIM, and PEN sites recorded all five mortality events. As the 1910 mortality was distributed across all sites and most logs were dated to that period we will refer to it as the 1910s outbreak to differentiate it from the less extensive events.

3.3. Duration of outbreaks

Mortality during the events occurred over several years at the affected sites, as is the norm with bark beetle outbreaks (Fig. 7). Mountain pine beetle-killed logs died in 1878 at the GRR site and in 1879 at the CAM site, and indicated the beginning of the mortality event centered around 1889. Based on the timeframe from the earliest to the latest death dates identified across all sites, the 1889 event lasted for 22 years, the 1910 outbreak lasted for 19 years, the 1945 event lasted for 10 years, the 1987 event lasted for 7 years and the 2012 outbreak lasted for 10 years (Table A.1). The 1868 event was only detected from two logs with death dates in consecutive years. Although death dates associated with the 1889 and 1910 events approached convergence around 1900, the distributions of dates did not overlap at any of the sites.

3.4. Age and size of mountain pine beetle-killed trees

The mean age of trees killed across all mortality events and sites was

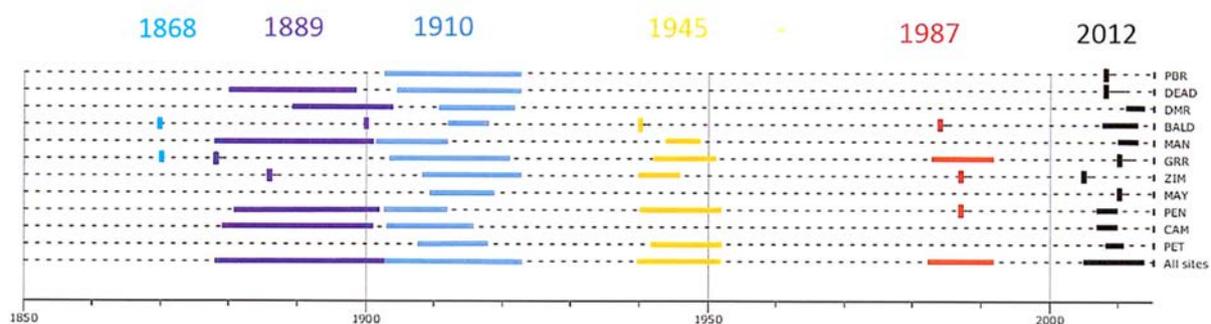


Fig. 7. Occurrence and duration of mountain pine beetle-caused tree mortality events identified at each site. Dashed horizontal lines represent the tree-ring timelines from 1850 to the present for each site. Colored bands along the timeline represent the duration of mortality events based on the earliest and most recent mountain pine beetle-killed death dates at each site. The shorter vertical lines represent a single log.



Fig. 8. Distribution of sites affected by mountain pine beetle during five mortality events. Year of event is noted in the upper right corner. Site names with squares around indicate affected sites during the mortality period. Outbreaks in 1910 and 2012 affected all sites.

232 (4.7) years with a median of 231 years including MPB-killed logs and dead trees sampled from the 2000s event (n = 186). Mean mortality age was > 200 years during the 1889, 1910, 1987, and 2012 events, and just under 200 years in 1945 (Fig. 9). There were no significant differences in the age of MPB-killed logs among the mortality events. Since only two MPB-killed logs were detected from the 1868 mortality event, and five trees from the 1987 mortality event, these were excluded from the analysis. The ages of individual trees killed by MPB ranged from 58 years in ZIM to 433 years at BALD. The mean age of MPB-killed trees was > 200 years in every site except ZIM (Table A.2). Lastly, the mean age of live trees between 20.3 cm and 25.4 cm, the size at which lodgepole pine becomes a suitable host for mountain pine beetle, was 196.3 (14.3) years (n = 31) (Table A.3).

The mean dbh of MPB-killed sampled trees for all sites and events combined was 35.8 (1.0) cm (n = 140; trees for which dbh was measurable), with a range from 20.9 cm at ZIM to 100.8 cm at GRR and a median of 33.0 cm. There were no significant differences in mean dbh of MPB-killed trees among mortality events; mean dbh was > 34 for all mortality events (Fig. 9). Again, since only two MPB-killed logs were detected in the 1868 mortality event and 5 MPB-killed logs were identified 1987 mortality event (only four with dbh data), these were excluded from the analysis. The mean dbh of MPB-killed trees across all mortality events was > 30 cm at all sites, well within the range of tree sizes considered suitable for MPB attack (Table A.2).

4. Discussion

4.1. Methodology and past mortality events

The use of identifiable signs of MPB activity on logs proved to be a reliable approach for reconstructing past mortality events. Signs were easily recognizable in the field and all MPB-killed logs sampled were successfully crossdated using standard dendrochronological techniques. The earliest death date determined for a MPB-killed tree was 1868 at the BALD site, which was 144 years before the beginning of the study. Older MPB-killed logs may have been present in the sites, but were fortuitously not selected for sampling or if identified as MPB-killed, lacked complete sapwood and bark and were not sampled as it was unlikely that an accurate death date could have been determined using our methods. For future studies, it might be possible to estimate death dates on such logs by developing an algorithm based on sapwood growth rates to reconstruct missing sapwood.

Direct evidence of past MPB infestation allowed identification of five mortality events in the northern CFR prior to the 2000s outbreak. The number of study sites affected, and their geographic distribution varied among the mortality events. All of our sampling sites experienced MPB-caused tree mortality synchronously during both the 1910 and 2012 events. This suggests that at least one widely distributed MPB outbreak occurred within the study area in the past 140 years. This timeframe is consistent with a study west of the Continental Divide discussed below.

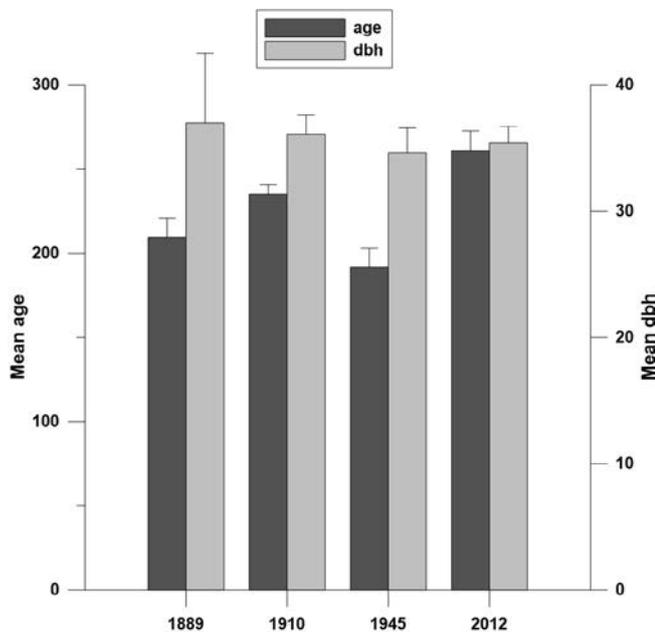


Fig. 9. Mean age and diameter at breast height (dbh) of mountain pine beetle-killed lodgepole pines during each mortality event across all sites. No significant differences were observed for either variable, Tukey-Kramer studentized test at $p = 0.05$. The 1868 mortality event was excluded from both analysis as it included only 2 trees (mean age = 226 years, SE = 60.0 years; mean dbh = 43.2 cm, SE = 7.6 cm). The 1987 mortality event was also excluded from both analysis as it included only 5 trees with age and 4 trees with dbh (mean age = 213 years, SE = 39.0 years; mean dbh = 49.0 cm, SE = 9.4 cm). Error bars represent standard errors. N for age = 24 for 1889, 98 for 1910, 23 for 1945, and 41 for 2012; N for dbh = 14 for 1889, 71 for 1910, 18 for 1945, and 37 for 2012.

There are few studies in the southern Rocky Mountains that we can use to compare our results. A study conducted along Independence Pass (IP), west of the Continental Divide in Colorado and approximately 200 km SSW from our study area, used growth releases from live trees to reconstruct MPB outbreaks (Jarvis and Kulakowski, 2015). Core samples from 10 sites detected MPB mortality at single sites in 1660, 1680, and 1710; at 4–7 sites in 1760, 1780–1790, 1810–1830, and 1860; at 2 sites in 1940–1945; and at all sites in 1910, 1965, and 1985. The earlier outbreaks were primarily detected through growth releases dated in 1 or 2 trees, while the later dates were based on releases with confirmed presence of MPB-galleries and blue stain in the cores. Other partial reconstructions also report MPB-caused tree mortality in western Colorado in the 1940s and 1980s (Kulakowski and Jarvis, 2011; Kulakowski et al., 2012).

When the findings of these studies and ours are considered together, a pattern of widely distributed MPB outbreaks occurred on both sides of the Continental Divide in the 1910s and the 2000s (the latter now well documented), with more geographically-limited events or low-level MPB-caused tree mortality in between. The historical timeframe of MPB activity reconstructed in our study that overlaps with the timeline of the IP study indicates concurrent MPB-caused tree mortality in the 1860s, 1910s, 1940s, 1985–1987, and the 2000s outbreak. Two periods of mortality differ between the studies; mortality in the 1890s in the CFR was not seen in the IP study, and mortality in 1965 in the IP study was not seen in the CFR. In addition, the 1985 mortality in IP affected all sites while only 4 of our sites experienced mortality and only a few MPB-killed trees were identified.

The availability of large areas of forest established in synchrony that reach susceptibility to MPB simultaneously is a major factor that can foster large or extensive mortality as observed in the 1910s and the early 2000s outbreaks. Other processes that influence MPB populations

and host trees are also needed to facilitate large outbreaks. Cold winter temperatures are a primary mortality agent for MPB (Amman, 1973; Régnière and Bentz, 2007; Reid, 1963). Periods of non-lethal winter temperatures increase survival of MPB populations that can then exploit an abundance of susceptible trees (Bentz et al., 2010). An inciting factor such as a drought that results in tree stress and compromised defenses can allow incipient MPB populations to increase to epidemic levels (Kolb et al., 2016; Mattson and Haack, 1987; Negrón and Cain, 2019). Both the 1910 and the 2012 outbreaks sampled in this study occurred in sites comprised of old, post-fire stands of abundant susceptible trees during or following significant drought conditions with endemic populations active, particularly in 1889. The Palmer Drought Severity Index in the area was between -4 to -5 in 1901–1902 and -3 to -6 in 2000–2003, the years preceding these extensive outbreaks (<https://www.ncdc.noaa.gov>; accessed May 2020) (Fig. A.2).

In contrast, the limited extent of the mortality in the 1868, 1945, and 1987 events in the CFR is likely the expression of low-level or incipient MPB populations functioning in these sites (Sibold et al., 2007). During these mortality events, not all sites were affected. In addition, during the 1889 event, most mortality was observed from the CAM site. Of the sampled trees that died in the 2000s outbreak in stands unaffected in 1945 and 1987, 54% and 77%, respectively, were older than 196 years at the time. This is the age when trees in the CFR become susceptible to MPB. This indicates the presence of suitable tree for MPB attacks during these events. If endemic bark beetle populations are present, a release of insect populations may result from factors such as fluctuating natural enemies' populations, mild winter temperatures, or density-dependent insect population dynamics factors with the potential to foster epidemic levels. Yet, if trees are growing vigorously and are not under the stress of large-scale inciting factors like a drought, beetle populations may not be able to increase and will only cause low or localized levels of tree mortality. Near-normal precipitation occurred in the 4 years prior to 1945, and precipitation was above normal in the 6 years prior to 1987, perhaps contributing to the limited mortality observed during these events in the CFR (Fig. A.2).

4.2. MPB mortality event characteristics

The duration of the 2000s outbreak in our study area was not different from past events. Historical mortality event duration in our study area was variable and, within our study area, the 1910s outbreak lasted longer than the 2000s outbreak. The 1889 mortality event and the 1910s outbreak lasted twice as long as the most recent events. This does not appear to be a function of the number of samples as similar numbers of samples were collected from all sites, even though some sites were larger. It does not appear to be related to whether populations were at endemic or epidemic levels. For example, the 1945 and 1987 events were likely associated with endemic populations and lasted as long as the 2000s outbreak. During an outbreak, beetles move from stand to stand, being active in a stand until most suitable hosts have been killed or the infestation collapses due to factors such as changes in environmental conditions that affect beetle populations or trees, or both. For example, as the canopy opens beetles seek more shaded environments even when suitable stressed trees are available for attack (Negrón, 2019). This explains the differential duration of mortality among stands. At the landscape scale, the 2000s outbreak in Colorado started in about 1997 west of the Continental Divide, with peak mortality reported in 2008 and MPB populations returning to endemic levels by about 2014, overall comprising about 17 years. Our sites were on the eastern edge of the 2000s outbreak and the recent mortality in our sites occurred during the latter part of the outbreak, centering around 2012. Additional sampling needs to be conducted to better assess what other factors may be influencing outbreak duration. How long an outbreak or mortality event lasts varies depending on the size of the area being considered (Schmid and Mata, 1996), the abundance of suitable host type, and insect population dynamics. At a stand scale, MPB outbreaks

in lodgepole pine usually last less than 10 years, while at the landscape scale an overall outbreak can last up to 3 decades (Amman and Schmid, 1992; Cole and Amman, 1980). The generalized return interval for MPB activity in a stand may be about 50 years, with a range of 20–120 years (Amman and Schmid, 1992; Jarvis and Kulakowski, 2015). The time between mortality events in this study falls within the ranges previously reported.

Mountain pine beetle-caused lodgepole pine tree mortality has been reported from the southern Rockies through Montana up to British Columbia from the 1890s through the 1920s as a single event (Alfaro et al., 2004; Jarvis and Kulakowski, 2015; Taylor and Carroll, 2004; Taylor et al., 2006). In the northern CFR, this mortality period may represent two separate events based on our data as we saw no overlapping mortality dates in any of our sites. This is also the case from the Teton National Forest in Wyoming and from Utah where the 1890s event is reported as a single event (Roe and Amman, 1970; Thorne, 1935). We detected the 1889 mortality event in 7 sites, though the mortality was most pronounced at CAM where 9 out of the 24 MPB-killed logs died during that event. All of these sites were also affected by the 1910 mortality event. Possibly an incipient population was present prior to and around 1889 and caused localized mortality but did not erupt due to the lack of an inciting factor. Insect populations may have increased again in the early 1900s as a result of a regional drought, as indicated above, that allowed the population to erupt. It is also possible our sampling fortuitously did not include logs indicating overlap. The 1868 mortality was based on only two trees. It likely represents endemic populations or it is possible that this may be about as far as our methods are viable, about 150 years. We do consider it a mortality event as mortality at the time has also been reported from other locations including Colorado (Jarvis and Kulakowski, 2015), Utah (Thorne, 1935) and in British Columbia (Hrinkevich and Lewis, 2011; Axelson et al., 2010).

The mean dbh of MPB-killed logs and trees across all events was 36 cm and the smallest tree killed was 21 cm. In the Intermountain Region and western Canada beetles prefer to attack trees > 20 cm in dbh and about 80–120 years old (Amman et al., 1977; Safranyik et al., 1974; Taylor and Carroll, 2004). In our study, site it takes a lodgepole pine 196 years to reach 20–25 cm in dbh, the low end of tree size susceptible to MPB (Table A.3). This is consistent with the work of Kauffmann (1996) who reported that lodgepole pine trees in Colorado about 31 cm in dbh, ranged in age from 250 to 296 years. The mean age of our MPB-killed logs was 232 years with a median of 231 years, showing that MPB-killed trees in our CFR sites were much older than those in other locations, presenting a very different temporal pattern. Kulakowski et al. (2012) suggested a “threshold” when stands may become susceptible to MPB at about 100–150 years. Their study sites originated primarily between the early 1700s to the late 1800s while our sites date from the early 1500s to the mid-1700s. The older age at which trees become more susceptible to MPB in the CFR along with overall older stands in our study sites may account for the partial differences in the history of MPB-caused tree mortality.

5. Concluding remarks

The approach used in this study allowed us to determine when the trees were killed to within a couple of years at most when the outer bark was still present somewhere on the log. Using the direct evidence of death dates limits the length of the reconstruction because the evidence in the form of intact sapwood eventually rots away, but is likely to be more accurate in assigning MPB as the driver of mortality. Growth releases can provide a longer record, but in the absence of other evidence need to be interpreted with caution. Both methodologies can complement one another to increase the length and accuracy of a reconstruction. Using multiple proxies, such as death dates, scars, historical records, climate records, and growth releases can create a better picture of the history of a stand including interactions with past fires.

The CFR, like parts of western Colorado and along the Rockies to British Columbia, has a long history of MPB outbreaks. These events may be synchronous across western North America (Jarvis and Kulakowski, 2015), especially in landscapes with large contiguous areas of suitable host trees, such as those that result from historical stand-replacing fires, and in conjunction with regional-scale droughts. Using historical records and proxy reconstructions, MPB outbreaks have been reported in multiple locations from the Southern Rockies to British Columbia dating from the mid-1800s (Alfaro et al., 2004; Axelson et al., 2009, 2010; Hrinkevich and Lewis, 2011; Jarvis and Kulakowski, 2015). The periods of MPB mortality that we detected in the CFR in this study have also been reported in other locations throughout the range of lodgepole pine and MPB (Axelson et al. 2009, 2010; Hrinkevich and Lewis, 2011; Jarvis and Kulakowski, 2015; Thorne, 1935). Endemic mortality levels and other localized disturbances occurred between the larger-scale outbreaks, fostering multi-cohort stands (Sibold et al., 2007). Our data sheds light on the historical occurrence of MPB outbreaks in the northern CFR and the tree age and size most frequently attacked. Like previous events, the 2000s outbreak occurred throughout the elevational range of lodgepole pine, up to at least 3250 m, with a spatial extent similar to that of the 1910s outbreak, at least within our study area, and may have been temporally shorter than the 1910s outbreak.

The effects of the 2000s outbreak on understory release and regeneration remain to be seen, but like the 1910s outbreak, it did not kill all the suitable-sized trees in the stands it affected (Klutsch et al., 2009), leaving legacies of past disturbances. Whether such events will become more or less frequent with a changing climate remains to be seen. While triggering events such as warmer winters and drought may become more frequent, it is unknown whether warmer conditions will encourage tree growth or speed the development of stands to MPB-susceptible stages.

Informed anticipation of future dynamics of disturbance interactions under novel climate conditions need to consider the past history of these events. The strength of the method we used to reconstruct historical MPB mortality is that it uses direct evidence of MPB attacks that reflect the insect’s biology to identify and date past outbreaks within a few years of their occurrence. Future reconstructions would benefit from collecting more complete age structure data in stands, sampling downed trees that show evidence of MPB attacks in combination with growth release data from surviving trees, and seeking evidence of a more complete disturbance history in stands including historical fires. Spatially distributed MPB outbreaks are not new to lodgepole pine forests in the CFR. Yet more frequent and intense droughts and fires and increased temperatures and possible changes in precipitation patterns associated with climate change are likely to interact with insect populations in novel ways (Jactel et al., 2019; Pureswaran et al., 2018; Schoennagel et al., 2003; Turner, 2010). Continuing our examination of interacting disturbances will lead to a better understanding of forest stand development and inform future management strategies to maintain sustainable and resilient ecosystems.

6. Author contributions

José F. Negrón: Conceptualization, field work, data analysis, writing of original draft, data archiving.

Laurie Huckaby: Field work, tree ring analysis, contributions to original draft, figures, and editing.

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8. Data availability

All data are archived at the USDA Forest Service, Rocky Mountain Research Station and are available with no restrictions as: Negrón, José F. 2020. Reconstructing historical outbreaks of mountain pine beetle in lodgepole pine forests in the Colorado Front Range. Fort Collins, CO: Forest Service Research Data Archive. <https://doi.org/10.2737/RDS-2020-0036>.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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