An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality

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Abstract. An innovative aerial survey method called the Landscape Assessment System (LAS) was used to assess mountain pine beetle (MPB; *Dendroctonus ponderosae*)-caused mortality of whitebark pine (*Pinus albicaulis*) across the species distribution in the Greater Yellowstone Ecosystem (GYE; 894 774 ha). This large-scale implementation of the LAS method consisted of 8673 km of flight lines, along which 4653 geo-tagged, oblique aerial photos were captured at the catchment level (a subset of 12-digit USGS hydrologic units) and geographic information system (GIS) processed. The Mountain Pine Beetle-caused Mortality Rating System, a landscape-scale classification system designed specifically to measure the cumulative effects of recent and older MPB attacks on whitebark pine, was used to classify mortality with a rating from 0 to 6 based on the amount of red (recent attack) and gray (old attack) trees visible. The approach achieved a photo inventory of 79% of the GYE whitebark pine distribution. For the remaining 21%, mortality levels were estimated based on an interpolated surface. Results that combine the photo-inventoried and interpolated mortality indicate that nearly half (46%) of the GYE whitebark pine distribution showed severe mortality (3–4 or 5.3–5.4 rating), 36% showed moderate mortality (2–2.9 rating), 13% showed low mortality (1–1.9 rating), and 5% showed trace levels of mortality (0–0.9). These results reveal that the proliferation of MPB in the subalpine zone of the GYE due to climate warming has led to whitebark pine mortality that is more severe and widespread than indicated from either previous modeling research or USDA Forest Service Aerial Detection surveys. Sixteen of the 22 major mountain ranges of the GYE have experienced widespread moderate-to-severe mortality. The majority of catchments in the other six mountain ranges show low-to-moderate mortality. Refugia from MPB outbreaks, at least for now, also exist and correspond to locations that have colder microclimates. The spatially explicit mortality information produced by this project has helped forest managers develop and implement conservation strategies that include both preservation and restoration efforts. Future research aimed at documenting and quantifying the ecological impacts of widespread decline and collapse of this foundation and keystone species is warranted.

Key words: aerial survey method; climate change impacts; Cronartium ribicola; Dendroctonus ponderosae; *geographic information system, GIS; Greater Yellowstone Ecosystem; Mountain pine beetle; pest monitoring;* Pinus albicaulis; *rapid assessment system; whitebark pine; white pine bluster rust.*

INTRODUCTION

The Greater Yellowstone Ecosystem (GYE) is an ecological reserve of regional, national, and international significance (Fig. 1). This collection of national parks, national forests, wildlife refuges, and tribal lands is generally recognized as one of the last remaining large, nearly intact ecosystems in the earth's northern temperate region (Keiter and Boyce 1991). Throughout the GYE, at elevations greater than ~2000 m, coniferous forests are the dominant land cover (Marston and Anderson 1991). Approximately 80% of Yellowstone National Park (YNP), which lies in the center of the

GYE and encompasses ~9000 km² of predominantly high-elevation (2100–2700 m) volcanic plateau with relatively mild topography, is covered by forests of lodgepole pine *Pinus contorta latifolia* (Romme et al. 2011). Outside the Yellowstone Plateau, the GYE's topography is much more rugged and consists of 22 major mountain ranges with semiarid river valleys in between. Douglas-fir (*Pseudotsuga menziesiia glauca*) and lodgepole pine are the most common species in the GYE montane zone, between 2000 m and 2500 m (Marston and Anderson 1991), while whitebark pine (*Pinus albicaulis*), the focal species of this study, dominates drier and more exposed slopes of the subalpine zone (above ~2500 m). On wetter, less exposed sites, whitebark is a major species, but is successively replaced by shade-tolerant subalpine fir (*Abies lasiocarpa*) or Engelmann spruce (*Picea engel-*
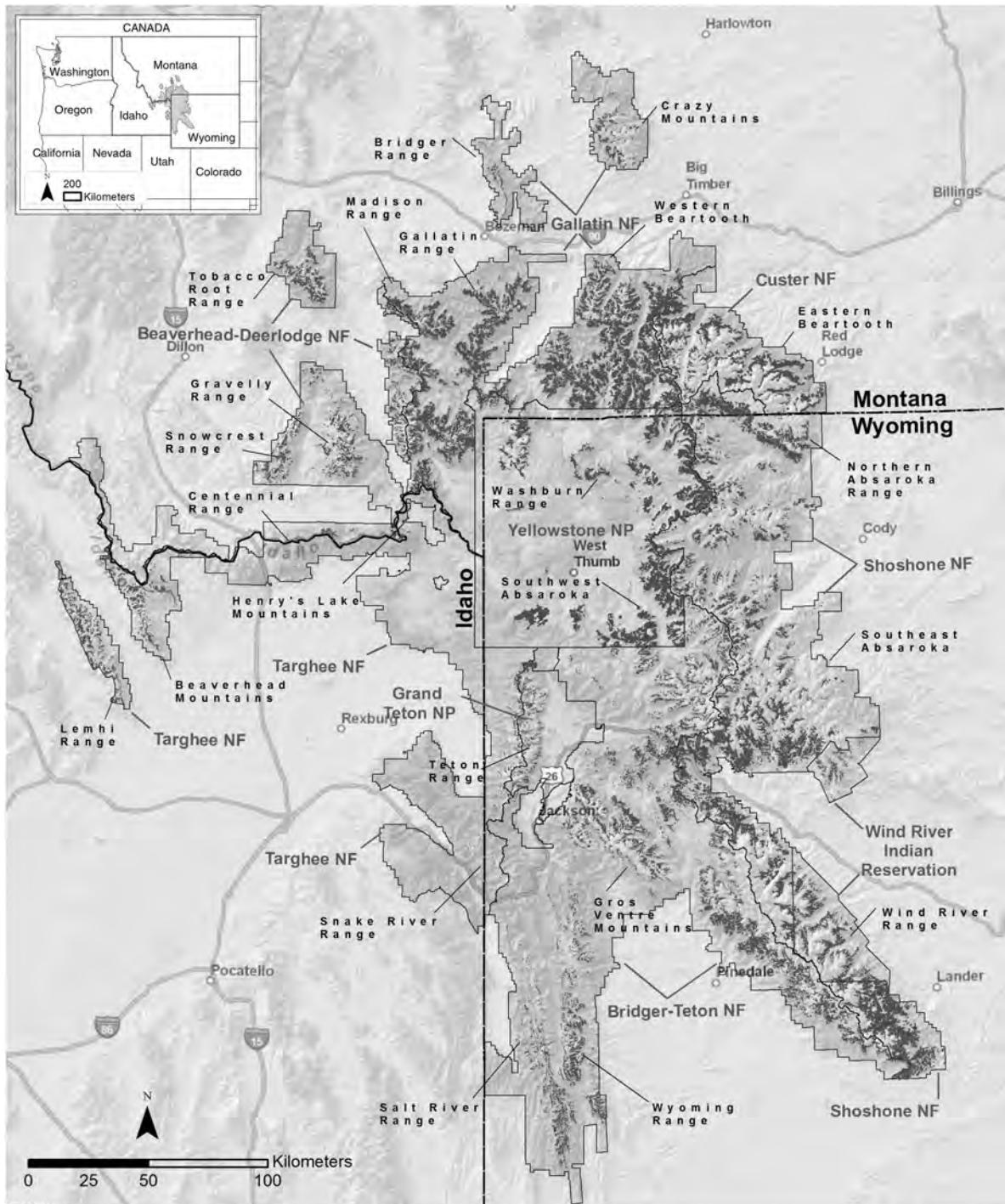
FIG. 1.   The Greater Yellowstone Ecosystem (GYE), located in south-central Montana, northwest Wyoming, and southeast Idaho, USA, covering ~59 000 km² of mountainous terrain. Displayed are the administrative areas of the GYE, including two national parks (NP) and six national forests (NF). The GYE's 22 major mountain ranges are identified, and the whitebark pine (*Pinus albicaulis*) distribution is shown in dark gray (894 774 ha).

mannii). At the upper end of the subalpine zone, whitebark pine is dominant (Despain 1990), and extensive contiguous climax forests are found on each of the 22 major mountain ranges of the GYE (Fig. 1).

According to the 2010 Whitebark Pine Distribution Map (2011) compiled by the Greater Yellowstone Coordinating Committee (GYCC) Whitebark Pine Subcommittee, there are an estimated 1 023 175 ha of

whitebark pine within the GYE, representing roughly 18% of the land cover (*available online*).[6]

Whitebark pine functions as both a foundation and a keystone species in the high elevations of the GYE (Tomback et al. 2001, Ellison et al. 2005, Resler and Tomback 2008). It forms the foundation of the subalpine zone by colonizing sites with difficult growing conditions. Once established, whitebark pine enhances soil formation and improves site conditions, enabling other conifer species to establish (Callaway 1998). At the landscape scale, healthy whitebark pine forests help regulate snow capture and retention, thus increasing the quantity and duration of summer runoff (Farnes 1989). Whitebark pine's large, highly nutritious seeds are critically important for a wide array of wildlife, including Clark's Nutcrackers (*Nucifraga columbiana*; Tomback 1978), red squirrels (*Tamiasciurus hudsonicus*; Podruzny et al. 1999), as well as black bears (*Ursus americanus*) and the iconic Yellowstone grizzly bears (*Ursus arctos horribilis*; Kendall 1983, Kendall and Arno 1990, Mattson and Reinhart 1994, Lorenz et al. 2008, Tomback et al. 2001). A review of the unique role whitebark pine plays in the GYE can be found in Logan and Macfarlane (2010).

Historically, the range of the mountain pine beetle (MBP; *Dendroctonus ponderosae*) was limited primarily to lower elevation forests because of the unfavorable climatic conditions found at higher elevations (Amman 1973). For this reason, whitebark pine forests have largely avoided past MPB outbreaks. Although widespread tree mortality did occasionally occur during periods of unusually warm weather (e.g., the 1930s), these past outbreaks were short lived and limited in scale (Ciesla and Furniss 1975, Perkins and Swetnam 1996) compared to the current outbreak in the GYE.

Since 1999, a warming climate in the Northern Rockies (Mote et al. 2005, Westerling et al. 2006) has coincided with MPB eruptions that have exceeded the frequencies, impacts, and ranges documented during the previous 125 years (Raffa et al. 2008). In particular, warming temperatures have allowed MPB to thrive in previously inhospitable whitebark pine forests. Several studies have shown that whitebark pine is highly susceptible to infestation by the MPB (Logan and Powell 2004, Six and Adams 2007, Bockino and Tinker 2012). In 1999, the annual USDA Forest Service's Aerial Detection Survey (ADS) of the GYE recorded only 217 ha of MPB-infested whitebark pine, but by 2007 the infestation levels had increased 320-fold to 69 433 ha (Gibson et al. 2008, Logan et al. 2009).

However, for a number of reasons related to the ADS mission, ADS may not be an adequate measure of GYE-wide whitebark pine mortality: (1) Priorities for areas to be flown are set at the national forest level and often reflect values (e.g., timber) other than the ecological services provided by whitebark pine, and as a result, appropriate funds are often not available for surveying whitebark pine habitat; (2) ADS is a "red top" survey, i.e., mortality estimates are limited to current red trees that result from successful beetle attack just the previous summer, and as a result, an individual year's survey does not represent a cumulative mortality estimate; (3) not every area is flown every year; (4) perhaps most importantly for the GYE, national parks and designated wilderness areas are not regularly flown. Approximately 62% of the whitebark pine distribution in the GYE is contained in either national parks or designated wilderness (Appendix A).

In 2008, motivated by a desire to more adequately document the mortality trend in GYE whitebark pine, a pilot study was initiated that combined a newly designed rapid assessment aerial survey system (Landscape Assessment System; LAS) and a prototype Mountain Pine Beetle Mortality Rating System (MPBM Rating System; *available online*).[7] In contrast to ADS, the MPBM rating system was designed to specifically measure the cumulative effects of current, recent, and older MPB attacks on whitebark pine rather than single-year mortality for all forest insects and pathogens. Recent mortality is evident by the large numbers of trees with red needles (symptomatic of trees killed the previous summer); older mortality is evident by red trees turning to gray as they lose their needles, leaving the residual ghost forest (Fig. 2; see Plate 1).

The pilot project demonstrated that LAS was a reliable monitoring technique capable of rapid assessment of both recent and older MPB impacts on whitebark pine in large, remote landscapes (Logan et al. 2009). The ability of the LAS method to quickly and affordably assess forest mortality attracted the attention of the GYCC Whitebark Pine Subcommittee and the USDA Forest Service's Forest Health Protection program, and in 2009, with the help from the Natural Resources Defense Council (NRDC), a LAS survey for the entire GYE was funded. The main objective of the project was to provide resource managers, for the first time, with a complete assessment of GYE-wide, MPB-caused whitebark pine mortality. The spatially explicit mortality information produced by this project was intended to help forest managers develop and implement conservation strategies that included both preservation and restoration efforts.

METHODS

The Landscape Assessment System (LAS)

LAS is an innovative rapid aerial survey assessment method that combines low-cost geo-tagged aerial photos and straightforward geographic information system (GIS)-based post-processing to photographically docu-

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[6] http://fedgycc.org/documents/WBPStrategyFINAL5.31.11.pdf

[7] http://www.fsl.orst.edu/wfiwc/awards/speeches/logan-address.pdf

Fig. 2. Repeat photos of the Avalanche Peak area looking toward Hoyt Peak near the East Entrance of Yellowstone National Park. (A) The upper photo was taken in 2005 and shows active widespread mountain pine beetle (MPB; *Dendroctonus ponderosae*)-caused whitebark pine mortality. (B) The lower photo was captured in 2011 and shows a residual forest post-outbreak. (C) The photo insert is a tourist photo downloaded from the internet, taken in 1995; back when, in the words of Thomas Turiano, the trail to Avalanche Peak led through "a beautiful forest of whitebark pine . . ." (Turiano 2003:240–241). Photo credits: (A) J. A. Hicke; (B) W. W. Macfarlane; (C) David Hodge.

ment and then map landscape-level conditions. The geo-tagged photos had precise geographic coordinates that permitted them to be easily and precisely positioned on a map. In this application, ecological condition was assessed using the MPBM Rating System by which researchers manually assigned a numeric (0–5.4) mortality rating based on the proportion of dead trees visible in each aerial photo (Appendix D).

Results from our pilot study (Logan et al. 2009) indicated the LAS aerial survey-based approach was an effective means to assess and document MPB-caused whitebark pine mortality in the GYE for the following reasons: (1) Reliable GYE-wide whitebark pine distribution layers are available and can be used to help identify whitebark pine forests from the air (Landenburger et al. 2008). (2) GYE whitebark pine follows a predictable elevational distribution: In the northern portion of the GYE, it generally occurs above ~2500 m, and in the southern portion it occurs above ~2800 m; therefore, onboard GPS data could be used to help delineate whitebark pine forests from the air. (3) Whitebark pines have distinctive rounded and irregularly spreading crowns that are easily recognized and distinguished from other conifers, even from the air (Fig. 3). (4) MPB-caused mortality has an obvious signature because the needles on dead trees turn bright red during the summer following successful beetle attack. Red canopies are clearly visible from aircraft and easily captured with photography (Fig. 3). Older

mortality, likewise, is clearly distinguishable by its gray canopy (no needles). (5) In the aftermath of an outbreak, beetle-killed trees can be distinguished from high-intensity fire-killed trees (including more than one-quarter of Yellowstone National Park's whitebark pine zone that burned during the 1988 fires; Renkin and Despain 1992) because the fine material, other than needles, remains on the beetle-killed tree, giving it a distinctive appearance (Fig. 3). However, in areas of low-to-moderate intensity fire (i.e., heat killed), fine materials remain and look similar to the beetle-killed tree. Therefore, in these cases, wildfire perimeter maps (Landscape Fire and Resource Management Planning Tools Project [LANDFIRE] Rapid Refresh products) were used to exclude MPB as the mortality agent (LANDFIRE 2007; map *available online*).[8]

Oblique aerial photography

Photos captured at an oblique angle were collected for this project and used for analysis in conjunction with existing vertical imagery of the study area. We chose to collect oblique photographs for the following reasons: (1) Given a constant altitude, oblique aerial photos can cover a much larger area than vertical aerial photos; and (2) an oblique view of a forest in conjunction with a vertical view, obtained in this case from base imagery in Google Earth, provided the interpreter with comple-

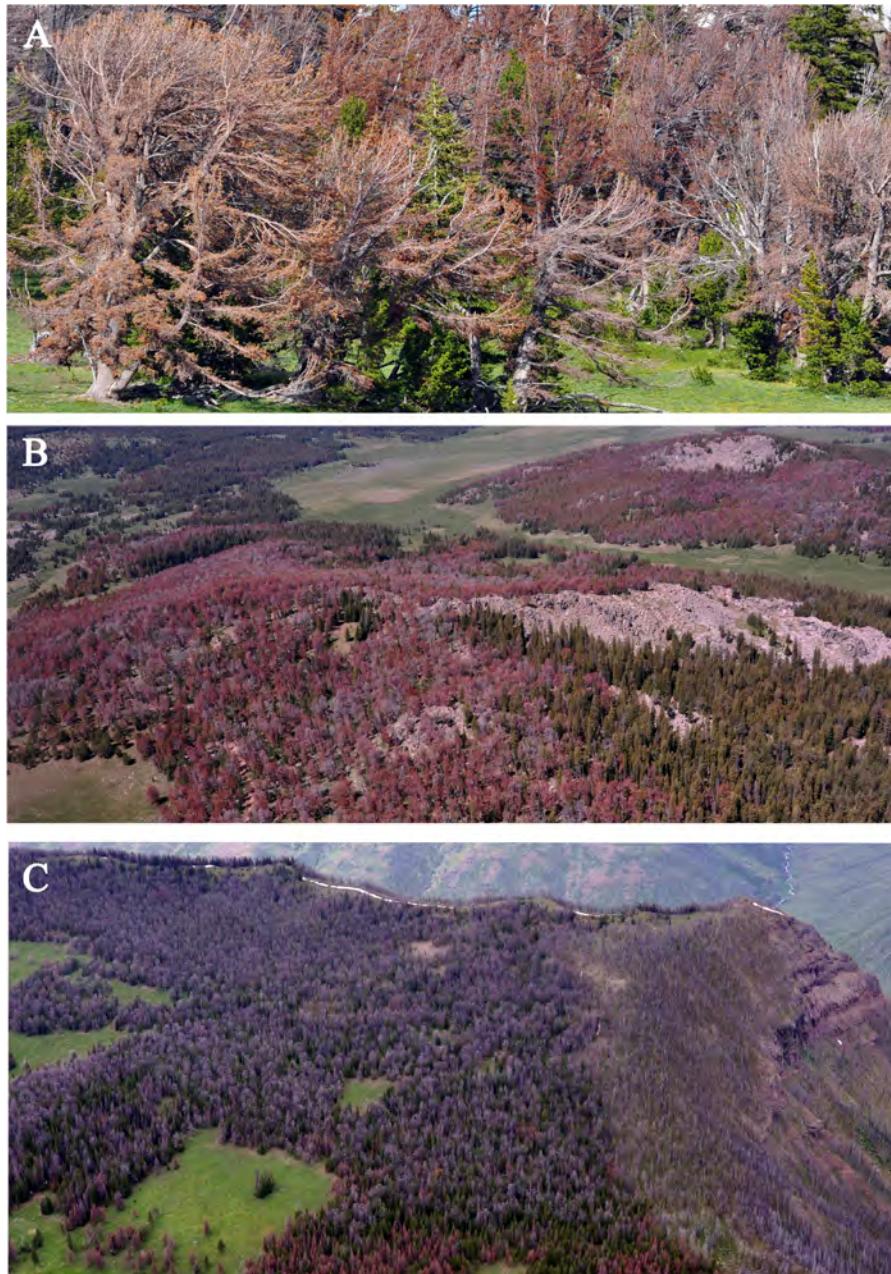[8] www.landfire.gov/updatedproducts_fireperimeter.php

Fig. 3. (A) The rounded and irregularly spreading crowns are common characteristics of whitebark pine (Union Pass, Gros Ventre Range). (B) Recent mortality is evident by large numbers of trees with red needles, which is symptomatic of trees killed the pervious summer (Union Pass, Gros Ventre Range). (C) The left side of the photo shows whitebark pine killed by MPB, with fine material remaining on the tree, and the right side shows trees killed by high intensity fire, with fine material burned off the tree (Yellowstone National Park). Photo credits: W. W. Macfarlane.

mentary views of forest structure, height, and understory and thus allowed for effective visualization of tree mortality. However, because oblique aerial photos distort perspective, specific measures were taken before the photos were used for GIS mapping purposes. This issue was resolved by capturing photos with Global Positioning System (GPS)-enabled cameras that embed (geo-tag) location information to each photo, and then each photo point was "spatially joined" to a corresponding catchment polygon (see *Overflights and oblique aerial photo capture* below).

LAS spatial scale

We determined that the catchment would serve as the project's minimum mapping unit (i.e., the smallest area unit to be mapped as a discrete entity; Lillesand and

Kiefer 1994) because this proved to be an effective management unit size for implementing conservation strategies. The catchment units are a subset of the subwatershed unit (12-digit U.S. Geological Survey [USGS] hydrologic units) and were delineated in ESRI ArcGIS 9.3 (ESRI 2009) based on a 30-m digital elevation model (DEM). Catchment size is directly related to topographic relief and complexity: The greater the relief and complexity, the smaller the catchment size. Over 70% of the GYE whitebark pine distribution is located in complex mountainous topography, and therefore the catchments in these landscapes are relatively small, ranging from 100 ha to 400 ha. The remainder of the GYE whitebark pine is distributed on high plateaus where the topography is less complex, and therefore the catchments are larger, ranging from 401 ha to 3000 ha.

LAS data collection and processing

The LAS data collection and processing workflow consisted of five steps: (1) flight line development, (2) overflights and oblique aerial photo capture, (3) image processing, (4) mortality assessment and mapping, and (5) ground verification.

Flight line development.—Flight lines were developed within Google Earth 5 Pro (2010 Google; *available online*)[9] by first identifying whitebark pine habitat using both the Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee (2011; see footnote 6) and the USGS (Landenburger et al. 2008) whitebark pine distribution maps, along with a 2500-m contour as background layers to ensure complete spatial coverage of all potential whitebark pine habitat. A system of parallel flight lines was developed for this habitat map, using a fixed parallel line interval of 8 km (Appendix B). This interval was used because our 2008 pilot study indicated an optimal 4–5 km width for this type of oblique photography. Therefore, with an observer on each side of the plane, an 8-km interval translated into each observer capturing a 4-km swath of forest on his/her respective side of the plane.

Flight lines were also delineated to run parallel to mountain ridges instead of over ridge crests, allowing for lower flight heights. This approach resulted in higher quality imagery, a better perspective to visualize and capture the catchments from the aerial perceptive, and a better perspective for post-processing three-dimensional viewing and analysis in Google Earth. Flight line data were transferred to both an onboard GPS used by the pilot for navigation, and to a handheld GPS unit used by the observers to record flight path information.

Overflights and oblique aerial photo capture.—Low-flying airplane overflights (300–1000 m above ground level) were conducted by EcoFlight, a nongovernmental organization (NGO) that facilitates conservation efforts by providing aerial support using a Cessna 210 Centurion airplane (more information *available online*).[10] A flight speed of ~44–46 m/s (85–90 knots) was used throughout the flights. Flight lines consisted of a total of 8673 km in length. The aerial survey required 55 hours of flying that were divided into 11 flight days. Each flight started and ended at the airport in Jackson, Wyoming, USA.

Nikon D5000 GPS-enabled digital single-lens reflex (SLR) cameras (Nikon, Tokyo, Japan) were used to capture the desired 12.5-megapixel, geo-tagged, oblique aerial photographs. A two-observer technique was used, with an observer seated on each side of the aircraft, each responsible for photo-documenting the whitebark pine visible from his/her position at the catchment spatial scale (Appendix C). Each photo captured had an associated GPS coordinate for the location and time at which the photo was taken, and this information was written in the exchangeable image file format (EXIF). Each geo-tagged photo was recorded as point data and later used to assign mortality ratings to polygon (catchment-level) data.

Image processing.—After each flight, the photos captured on that flight were transferred from the camera to a hard drive in both high-quality Jpeg and Raw format. An image viewing and editing program Picasa 3 (2010 Google; *available online*)[11] was used to examine each photo for image quality. Some images were visually improved using standard image enhancement techniques under the "Basic Fixes" tab (e.g., contrast, fill light, and brightness).

Then, RoboGEO version 5.6 (2003–2010 Pretek, *available online*)[12] was used to transfer the flightpath and tagged photos to keyhole markup language (KML) format for use in Google Earth. This processing step generated a point (x, y, and z coordinate) that identified the location of each photo along the flight line. We called these identifiers "photo points." In the small number of instances where photos were missing coordinates because the camera's GPS unit temporarily lost satellite reception, the handheld GPS unit's data was used to geo-tag photos. In Google Earth, the flight lines, photo points, and linked images were examined for spatial accuracy and spatial coverage on a three-dimensional globe. All photo point location errors were identified and fixed.

After the photo points were fine-tuned by the observer within Google Earth, a "snap shot" view was established. Generating the snap shot view was a manual process that required zooming to the precise location of each photo and framing the photo with the correct rotational angles provided by the Google Earth interface. The snap shot view, therefore, represented and saved the view that the camera "saw" when the oblique

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[9] www.earth.google.com

[10] http://www.ecoflight.info/
[11] www.picasa.google.com
[12] www.robogeo.com

PLATE 1. Close-up photograph of upper-elevation whitebark pine forest shown in Fig. 2. All mature, cone-bearing whitebark pine have been killed by mountain pine beetle. The future of this forest resides in understory seedlings and saplings that were too small for mountain pine beetle invasion during the current outbreak episode. This future, however, is uncertain with continued climate warming. Will these residual trees reach cone-bearing size, only to fall victim to future generations of mountain pine beetle? Photo credit: J. A. Logan.

photo was taken. Each photo's snap shot view provided the user with a three-dimensional visualization of the forest condition. This process also generated coordinates of the ground location for the center of each photo. These locations were called "look-at points."

Mortality assessment and mapping.—Mortality ratings were manually assigned by a team of four observers that used ongoing field-, laboratory-, and plane-based discussions to calibrate their mortality assessments at the catchment level. Mortality ratings were assigned during post-processing using workstations with dual high-definition flat-panel monitors. On one monitor, Google Earth was used to display the appropriate look-at point and associated pop-up low-resolution aerial photo. On the other monitor, Picasa 3 displayed the respective aerial high-resolution photo centered at the appropriate look-at point. Mortality levels were assigned at the catchment level by zooming in on the high-resolution photo, visually examining the photo for evidence of whitebark pine mortality, and then applying a single numeric (0–5.4) rating to both the photo and the associated look-at point based on the MPBM Rating System (Appendix D). In most cases, the same observer that took the photo made the mortality classification.

This MPBM Rating System ranks whitebark pine mortality based on the proportion of dead canopy visible in each aerial photo. In forests with active

outbreaks, the amount of red (recent attack) and gray (older attack) whitebark pine was visually assessed and rated. The active outbreak ratings ranged from 0 to 4, with fraction categories (in steps of 0.25) to describe variation within major categories. Areas where the outbreak cycle had ended (no remaining red trees) were classified as residual forests, with ratings from 5 through 5.4, depending upon the amount of remaining green whitebark pine visible in the photo (Table 1).

Both point and polygon whitebark pine mortality maps were generated in ArcGIS 9.3 (ESRI 2009). Point map generation consisted of plotting look-at points and associated mortality values onto a project area map. Polygon map generation involved a GIS process that consisted of spatially joining the look-at points and the catchment boundaries, then "clipping" the catchment extents by the whitebark pine distribution to form the catchment-level mortality map. For catchments not directly sampled by look-at points (21%), a "kriged" mortality surface was interpolated. In an effort to avoid overestimating mortality intensity across the interpolated mortality surface, the post-outbreak ratings (5.3, 5.325, 5.35, 5.375, and 5.4) that reflect both mortality intensity and outbreak timing were reclassified to their corresponding intensity values (3, 3.25, 3.5, 3.75, and 4, respectively). These reclassified values were added to the look-at point GIS layer and were used as the input

TABLE 1.   Numeric ratings and mortality levels associated with the Mountain Pine Beetle (*Dendroctonus ponderosae*) Mortality (MPBM) Rating System for whitebark pine (*Pinus albicaulis*).

Numeric rating	Mortality level	Description
0–0.75	trace	Green forest with trace levels of mortality. "Trace mortality" refers to a catchment that contains an occasional red tree but there is no evidence of mortality expanding to neighboring trees.
1–1.75	low	Green forest with occasional spots of red trees across the catchment. The increasing frequency of current-year red spots is assessed with a 1.25, 1.5, and 1.75 rating. Spots do not show evidence of multiyear mountain pine beetle-caused mortality.
2–2.75	moderate	Primarily green forest with multiple spots of red and/or gray trees across the catchment. Spots show evidence of two or more years of subsequent mortality. The increasing magnitude of these spots is assessed with a 2.25, 2.5, and 2.75 rating.
3–4	severe (active outbreak)	Primarily red forest where spots of red and gray trees have coalesced across the catchment. A catchment may display a varying degree of coalescing spots ranging from initial coalescence, category 3, to increasing coalescence that is assessed with a 3.25, 3.5, 3.75, and 4 rating, where essentially the entire whitebark pine overstory is red.
5.1–5.4	residual forest	Residual forest where a catchment may contain a varying degree of remaining green forest after a mountain pine beetle attack. This variation is captured with a 5.1–5.4 rating where virtually the entire whitebark pine overstory is dead and gray. These mortality intensity values are equivalent to those found in the 1–4 categories (i.e., a 5.35 rating is equal to a 3.5 at the end of the outbreak cycle). Rating of 5.x pertains to a residual forest, as opposed to a 1–4 that indicates the red-attack stage.

variable for kriging. Therefore, the final polygon-based mortality map consisted of a combination of sampled catchments that included both active and post-outbreak conditions (0–5.4) and non-sampled catchments that consisted of mortality intensity values (0–4). A recognized limitation of this approach was that, by using mortality intensity ratings only; the timing of post-outbreak condition for non-sampled catchments is not captured with the resulting interpolated mortality surface.

Precision and accuracy assessment.—Manual classification of MPB-caused mortality is inherently subjective because of observer variability that directly influences the repeatability (precision) of the resulting classifications. The precision of our classification method was assessed by randomly selecting a total of 465 aerial photos (10% of total photos), and then having two observers independently classify mortality by major mortality level (0, 1, 2, 3, 4, 5) in each photo. Cohen's kappa statistic (0–1) was used to measure agreement between the observers' classifications because it is more robust and conservative than the overall error rate (Congalton 1991). The accuracy of the LAS method was assessed by using a GIS viewshed analysis along roadways that access whitebark pine forests to identify and map a total of 300 potential ground-based classification viewpoints. Each of these ground verification viewpoints was physically visited, and an independent on-the-ground mortality classification was conducted and compared to the aerial photo-based classification. Cohen's kappa statistic was once again used to measure agreement between the on-the-ground and photo-based classifications.

Results

The LAS whitebark pine mortality assessment results are contained in three data formats: (1) aerial oblique photographs (KML point files with associated photo "pop-ups"), (2) look-at point mortality maps, and (3) polygon (catchment-level) mortality maps.

Oblique aerial photographs

The aerial perspective obtained from the LAS overflights provided an unobstructed view of the forest overstory that allowed for effective aerial photo-documentation of whitebark pine mortality. A total of 4653 oblique aerial photos were determined to be high enough quality for accurate mortality assessment. These photos were widely distributed along 8673 km of predetermined flight lines, covering all 22 major mountain ranges of the GYE. This extensive photo inventory documented whitebark pine mortality that was more severe and widespread than indicated from either previous modeling research or the USDA Forest Service Aerial Detection (Fig. 4). The higher than anticipated mortality emphasized the need for developing a comprehensive whitebark pine conservation strategy.

In an effort to aid resource managers in the development of such a strategy, the 4653 classified photos were processed to produce a KML file that allowed forest condition to be effectively evaluated in a spatially explicit three-dimensional context within Google Earth (Supplement). The resulting KML file provided a photographic record of whitebark pine condition for the GYE at a time (summer 2009) when the ecosystem was experiencing a MPB disturbance of historically unprecedented proportions, and established a base-line to evaluate both future
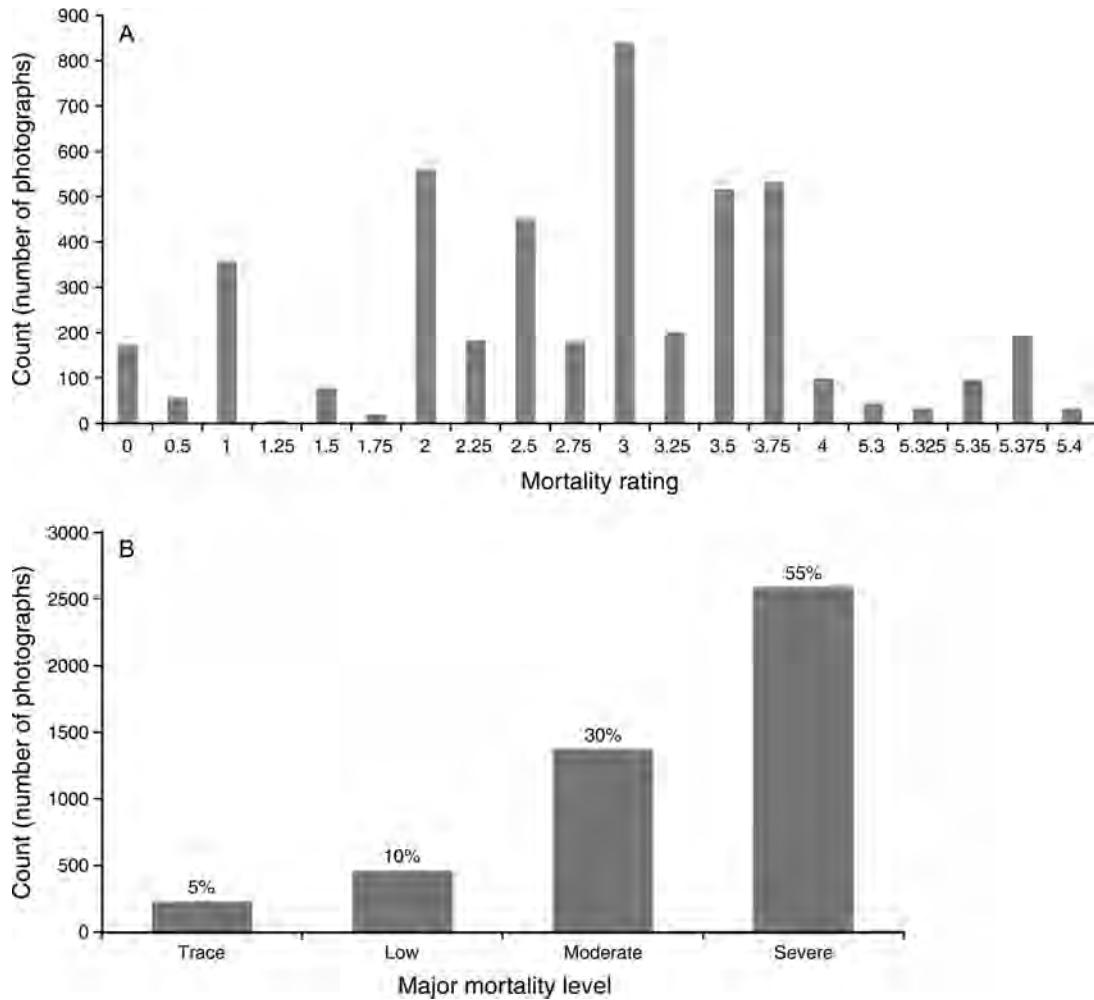
FIG. 4. (A) Frequency distribution of classified aerial photos ($n = 4653$ in total) by mortality rating: 0–0.75 represents trace level of mortality, 1–1.75 represents the occasional spot mortality, 2–2.75 represents multiple-spot mortality, 3–3.75 represents coalesced mortality, and 4 represents the removal of virtually all whitebark pine overstory. Residual forest ratings of 5.1–5.4 indicate a decreasing amount of green trees remaining after a mountain pine beetle attack, and a rating of 5.4 indicates a forest where essentially the entire whitebark pine overstory has been removed and turned gray. The residual forest ratings are equal in mortality intensity to the red-attack categories 1–4 (i.e., 5.5 is equivalent to 3.5 in mortality intensity). (B) Frequency distribution of classified aerial photos ($n = 4653$) with mortality ratings grouped into major mortality levels: trace level of mortality (0–0.75); low mortality (1–1.75); moderate mortality (2–2.75); and severe mortality (3–4 and 5.3–5.4). The percentage of the total for each level is shown above the bars.

outbreaks and potential regeneration/recovery of whitebark pine forests.

Look-at point-based mortality map

The look-at point-based mortality map showed the specific ground location of each photo and the corresponding mortality rating (0–5.4) and revealed clusters of mortality indicating strong autocorrelation (i.e., areas closer together are more likely to have the same level of mortality than those far apart; Fig. 5). The spatial scale of the mortality pattern exhibited by the point-based mortality assessment supports the hypothesis that outbreaks resulted from a simultaneous release of resident low-level MPB populations rather than an

invasion of outside sources. Additionally, the clustered point mortality pattern provides an indication of the temporal sequence of disturbance, with orange and red indicating either a building or peak outbreak, and gray indicating post-outbreak/residual forest. From this temporal pattern, the epicenter of the disturbance is apparently the east-central portion of Yellowstone National Park and the northwest part of the GYE. Throughout the entire GYE, all look-at points documenting residual (gray attack) forests were classified with severe (5.3 or greater) ratings, indicating that the current MPB infestations are consistently progressing to an outbreak stage before ending.

Catchment level mortality map

The GIS analysis revealed that the project's 4653 look-at points intersected with 3185 of the total 4862 catchments (73% by area). Another 657 catchments (6% by area) were identified as wildfire-dominated mortality and were excluded from the MPB-caused mortality analysis. For the remaining 1677 catchments (21% by area), a mortality surface was interpolated using kriging (Appendix E).

Kriging was determined to be appropriate based on the results of the Global Moran's *I* statistic and Ripley's *K* function. Computed values for the Global Moran's *I* statistic, which evaluated whether the mortality pattern expressed was clustered, dispersed, or random, indicated a statistically significant tendency toward clustering with a positive Moran's *I* index of 0.61. The Ripley's *K* function also indicated that the mortality look-at point data exhibited strong spatial dependence (feature clustering) over the entire GYE whitebark pine distribution. These results show strong spatial autocorrelation, so the data is appropriate for interpolation using kriging.

The photo-inventoried and interpolated catchment-level mortality data were combined to generate GYE-wide spatial mortality data. Similar to the point-based analysis, the catchment-level data revealed widespread moderate-to-severe whitebark pine mortality across the vast majority (82%) of the GYE (Fig. 6). The catchment-level mortality map delineated the spatial patterns of mortality and revealed widespread, severe ongoing, and post-outbreak whitebark pine mortality across the GYE distribution (Fig. 7). These foundation and keystone forests with severe ongoing or severe post-outbreak mortality are tending towards "functionally extinct," meaning they are no longer capable of providing the important ecosystem services they once did. Since GYE resource managers have determined that heavily impacted catchments are good candidates for restoration efforts, and less impacted areas are most suitable for preservation, the catchment-level mortality map identifies many opportunities for restoration across the GYE, but far fewer opportunities for preservation. Additionally, the catchment-level forest mortality corresponds to mircoclimate patterns (lower mortality in colder catchments and higher mortality in warmer catchments), thus supporting the assertion that the proliferation of MPB in the subalpine zone of the GYE is climate-warming driven.

Precision and accuracy assessment

Landis and Koch (1977) provide the following kappa ranges for strength of agreement: poor (0.00), slight (>0.00–0.20), fair (0.21–0.40), moderate (0.41–0.60), substantial (0.61–0.80), and almost perfect (0.81–1.00). The observed kappa statistic with linear weighting was 0.86, indicating almost perfect agreement between the MPBM Rating System classifications given by two independent, highly experienced observers to the 465 aerial photos (10% of total photos).

Of the 300 potential on-the-ground classification viewpoints that were identified and mapped, we found that 275 (or 91%) of these were easily accessible and provided an unobstructed view. These viewpoints allowed an effective comparison between mortality classifications based on aerial photos and observed on-the-ground classifications. From our viewpoints, the mortality conditions for 481 catchments (or 10% of the 4862 total LAS-surveyed catchments) were assessed by major mortality level (0, 1, 2, 3, 4, 5) resulting in the on-the-ground classification of roughly 12% of the GYE whitebark pine distribution (Appendix F). Once again the kappa statistic was used to quantify the degree of agreement between the mortality classifications of the aerial photographs compared to the on-the-ground classifications. The observed kappa statistic with linear weighting was 0.82, indicating a high level of agreement between on-the-ground classifications and those based on oblique aerial photos.

DISCUSSION

LAS summary

The extensive inventory of classified geo-tagged photos, spatial data sets, and mortality maps resulting from the LAS project provided important spatially explicit mortality information for the conservation of this foundation and keystone species. Results from this work have already provided resource managers with a useful tool for planning and implementing conservation strategies, and have provided a baseline of whitebark pine forest condition that can be used as a reference point to evaluate either the recovery or loss of whitebark pine forests following an unprecedented disturbance. LAS is a new approach to assessing MPB impact in whitebark pine forests that addresses limitations to previous methods like the ADS and satellite image analysis.

Similar to LAS, the ADS method utilizes low-level flights to map forest damage. In contrast to ADS, the LAS approach was designed to specifically measure the cumulative ecological impact of MPB on whitebark pine rather than seasonal mortality. As such, the traditional ADS approach is limited to documenting current red trees that result from successful beetle attack just the previous summer, and as a result, an individual year's survey does not represent a cumulative mortality estimate. Also, since not every area is flown every year, it is not possible to estimate cumulative mortality by simply summing year-to-year mortality. Additionally, the LAS approach provides a spatially accurate permanent photographic record of forest condition that can be externally evaluated (Supplement). In contrast, ADS observers use either digital or paper maps, typically 1:100 000-scale, upon which they hand sketch forest damage by drawing points and polygons attributed by damage type, defoliation intensity, or number of dead
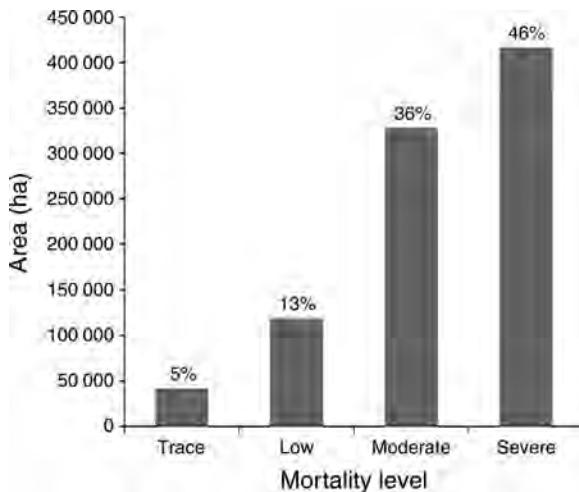
FIG. 5.   GYE-wide, point-based, whitebark pine mortality map. The map displays the location and associated rating (0–5.4) with fraction categories (in steps of 0.25) of all project oblique aerial photos ($n = 4653$). Areas of severe mortality, shown as clusters of points with shades of red and gray, indicate outbreak levels of MPB populations. Areas of moderate mortality, shown as clusters of points with shades of orange and yellow, indicate MPB populations that are in the initiating phase of the outbreak cycle. Healthy forests (points with shades of green) were clustered in the Wind River Range, the West slope of the Teton Range, and the Eastern Beartooth Plateau, indicating areas that, at least for the present, remain fully functioning whitebark pine forests. These areas of refuge from MPB outbreaks, at least for the time being, correspond to locations that have colder microclimates.

FIG. 6. Area calculations for small-catchment-level mortality ($n = 894\ 774$ ha total). Mortality ratings are grouped into major mortality levels: trace level of mortality (0–0.75), low mortality (1–1.75), moderate mortality (2–2.75), and severe mortality (3–4 and 5.3–5.4). The percentage of the total for each level is shown above the bars.

trees (McConnell et al. 2000). There is no convenient way for an independent observer to evaluate mortality classification from these maps. Moreover, ADS provides little information regarding what the residual stands "look like" following an outbreak; so even in areas where annual mortality levels have been recorded, it is difficult to determine the amount of live overstory whitebark pine remaining to assess recovery potential (Schwandt and Kegley 2008). Notwithstanding the limitations of annual ADS data, the method provided useful information on mortality trends that generally corroborated our LAS data.

Many remote-sensing studies have focused on detecting the red-attack stage of MPB outbreaks using satellite imagery with resolutions ranging from medium to very fine (Wulder et al. 2006a). Franklin et al. (2003), Skakun et al. (2003), and Wulder et al. (2006b) used Landsat imagery (30-m resolution) to achieve red-attack detection accuracies of 67–78%. Coops et al. (2006), White et al. (2005), Hicke and Logan (2009), and Wulder et al. (2008) used high-resolution imagery (2–4 m) and reported red-attack detection accuracies of 71–93%, while Meddens et al. (2011) reported that even finer resolution does not necessarily lead to better detection accuracy and found that 2.4-m resolution imagery provided the most accurate detection in lodgepole pine forests. The high classification accuracies make high-resolution satellite imagery a promising tool for assessing MPB-caused forest mortality. However, at the present time, non-archive high-resolution satellite imagery is cost prohibitive for large landscapes such as the GYE.

The high cost of acquiring current high-resolution imagery has made Landsat-based approaches the standard for GYE-wide mortality assessments. In 2008, the Remote Sensing Application Center (RSAC) used Landsat satellite imagery to detect canopy change in all conifer forests, using scenes from 2000, 2007, and 2008 across ~90% of the GYE (Goetz at el. 2009). Results indicate that 79% of the whitebark pine zone in the GYE showed some level of canopy change, and 27% showed "moderate" or "high" canopy change. This canopy change assessment did not provide information specific to mortality levels (i.e., amount dead or alive); rather it showed canopy change that was assumed to be related to mortality. While providing useful information, this satellite image analysis has inherent limitations. The 30-m Landsat resolution was too coarse to discern individual whitebark pine crowns or small clusters of affected trees and gray-attack detection was not possible. As discussed in the second paragraph of the *Discussion*, information on gray-attack locations can be important for assessing cumulative mortality, success of conservation efforts, and calculating MPB spread (Wulder et al. 2006a). At the present time, only expensive fine-resolution (0.5–2.4 m) multispectral imagery can detect the gray stage of forest mortality (Dennison et al. 2010, Meddens et al. 2011).

LAS, of course, has its own limitations, most notably the time and expense of training observers to categorize outbreak levels from photography, the labor-intensive step of orienting photos to look-at points, and the subjective nature of manually classifying MPB-caused mortality. Despite the respective identified limitations of the LAS, ADS, and satellite image analysis approaches, each method provides useful complementary information, and when used in aggregate, these methods can provide a more complete picture of whitebark pine decline in the GYE and connections with climate drivers. For example, Jewett et al. (2011) used a time series of nine images from 1999–2008 of Landsat satellite imagery to monitor whitebark pine mortality in the core of the GYE. Mortality patterns were analyzed with respect to monthly climate variations over the nine-year period. Historical high-resolution imagery available on Google Earth was used to confirm a relationship between visible red-attack whitebark pine stands and negative Landsat-derived "enhanced wetness difference index" (EWDI) values. Their results support our findings and indicate that drier and warmer climates are correlated with increased whitebark pine mortality, potentially due to increased mountain pine beetle activity.

Outbreak patterns: potential refugia

Of the 22 major mountain ranges in the GYE, our results identified some that were less impacted than others. We hypothesize that these less impacted mountain ranges may be more resistant to climate change than others, and therefore, may be more likely to avoid MPB impacts for the near future. The two areas most likely to provide effective refugia for whitebark pine are the
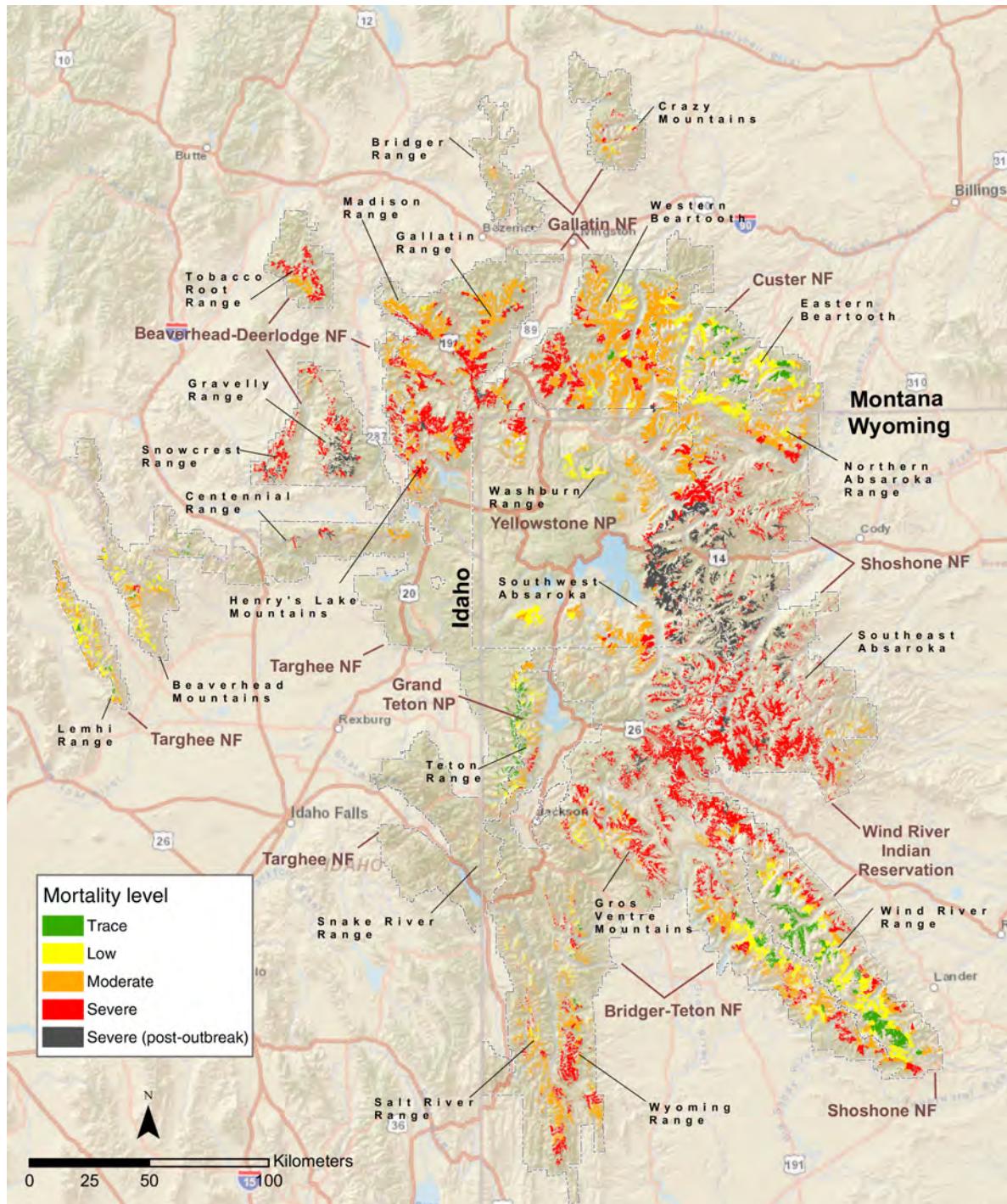
FIG. 7. GYE-wide whitebark pine distribution catchment-level mortality map. The map displays mortality ratings of all 4862 catchments (3185, or 79% by area, were photo-inventoried, and the remaining 1677, or 21%, were interpolated). Mortality ratings are grouped into major mortality levels: trace level of mortality (0–0.75, green), low mortality (1–1.75, yellow), moderate mortality (2–2.75, orange), severe mortality (3–4, red), and severe post-outbreak (5.3–5.4, gray). Catchments with severe ongoing and severe post-outbreak mortality levels dominate the map, indicating widespread decline and collapse of this foundation and keystone species in these areas.

central core of the Wind River Range in Wyoming and the Beartooth Plateau in Montana.

The Wind River Range's resistance to climate warming may result from being the highest mountain range in the GYE and having one of the most complex glacial systems in the contiguous U.S. Rocky Mountains (Holmes and Moss 1955). The moderating influence of high-mountains, permanent snow and ice may have resulted in a local climate that remains too harsh for development of outbreak MPB populations. However, this moderating influence may be short lived because glaciers in the Wind Rivers, like in Glacier National Park, are shrinking at a historically unprecedented rate. Thompson (2009) found a 42% decrease in the volume of glaciers in the Wind River Range between 1966 and 2006. Once the remaining permanent snow and ice is lost from these glaciers, we anticipate increased likelihood of a threshold event that will dramatically improve thermal habitat for MPB, and a concurrent increased outbreak potential.

The Beartooth Plateau is perhaps an even more promising refuge than the Wind River Range. The Beartooth Plateau is the largest contiguous area above 3000 m in the U.S. Rocky Mountains (Turiano 2003). This large, high plateau is extremely cold, with particularly long winters (Locke 1989). The combination of high elevation, cold temperature, and a short growing season has resulted in a vast expanse of dwarf/Krummholz whitebark pine forests. The long-term survival of the species likely resides in the Krummholtz growth form found throughout the ecosystem near tree line, because it is too small for beetles to attack, and because, over time, it is capable of assuming an upright growth form under more moderate climate conditions. Nevertheless, even these krummholz tree islands are susceptible to white pine blister rust and are already being impacted by this introduced pathogen (Resler and Tomback 2008).

Outbreak patterns: distribution across the landscape

LAS aerial photos consistently captured two different microclimate-driven patterns of MPB-caused mortality: (1) Higher intensity outbreaks tended to occur on the southern aspects (warmer and drier aspects) when compared to nearby northern aspects (colder and wetter aspects), and (2) mid-slope rather than lower-slope whitebark pine habitats were the first to become vulnerable to MPB.

The aspect-related mortality pattern is intuitive and suggests that the warmer microclimate on southern slopes allows the beetles to thrive in these sites first before spreading to cooler northern aspects (Logan et al. 2010). This mortality pattern is also apparent in areas where the outbreak cycle was further progressed, where southern-aspect red trees have already faded to gray and northern-aspect green trees have just turned red (Appendix G).

Conversely, the mid-slope mortality pattern (Appendix H) is counterintuitive because the MPB outbreak in whitebark pine is primarily driven by a warming climate and elevation lapse-rate models would predict that the lowest elevation habitat should be the first to become warm enough to support outbreak populations. We hypothesize that cold air pooling from temperature inversions, typical winter weather in these high mountain valleys, combined with lack of summer heat at the higher elevations are responsible for this counterintuitive phenomenon. The net effect is high winter MPB mortality in the cold valleys and insufficient thermal energy to complete an entire life cycle in one year at higher elevations. Further research could test this hypothesis and place results within a meaningful management context, such as identifying areas on the landscape that serve an "early-warning" function for impending outbreaks.

CONCLUSIONS

Results from our work indicate that the scope and severity of the current MPB outbreak in GYE whitebark pine are far beyond the episodic events of the historical past. The levels of ecosystem-wide forest mortality we found are more intensive and widespread than expected through model prediction (see footnote 7) or previously documented by ADS. We conclude that the LAS methodology we have developed adds a new dimension to evaluating the impact of increased MPB activity in whitebark pine. This technology has the potential for evaluating MPB activity in other whitebark pine habitats, as well as being more generally applicable for evaluating other ecological disturbances.

The documented mortality is alarming for a number of reasons. First, there are no signs that the climate change-induced conditions that have allowed the MPB to flourish will abate any time soon. It therefore appears likely that whitebark pine mortality will continue until the species has largely been removed from the GYE (U.S. Fish and Wildlife Service 2011). Second, indicators of the future health of the species, primarily seed production, recruitment, and regeneration, are being greatly reduced by the combined and synergistic effects of white pine blister rust and MPBs. Third, because whitebark pine is an exceptionally slow-growing species, and cone crops are not generally produced until 80 to 120 years of age (McCaughey and Tomback 2001), even under the best case scenario, the recovery of the species will likely take several centuries. Finally, future recovery of the species is in jeopardy because whitebark pine largely depends upon the Clark's Nutcracker for seed dispersal, whereas the Clark's Nutcracker, a facultative mutualist, will abandon subalpine forests during periods of cone shortages (McKinney et al. 2009); therefore, heavily impacted forests could be left with little means to regenerate. These results indicate a greater impact than previously was generally recognized or appreciated

(Greater Yellowstone Coordinating Committee White-bark Pine Subcommittee 2011; see footnote 6).

Resource managers are concerned and are beginning to respond to the whitebark pine crisis. A whitebark pine conservation strategy that includes preservation and restoration options, utilizing data from this project, has been developed (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee 2011; see footnote 6). Forest treatment proposals also are being formulated and implemented. We have two general concerns about the impending management responses: (1) The rapid, climate change-induced, alteration of high-elevation ecosystems is not being considered sufficiently under the current adaptive management strategies, and (2) almost everything we know about managing MPBs comes from experience in lodgepole pine forests, and the ecological functionality of MPB in whitebark pine is radically different from that in lodgepole pine.

Our results support an urgent need for more research and an improved interplay between research and management. A prospective, rather than reactive, management view is needed in order to respond to the climate change-driven collapse of the whitebark pine ecosystem. In addition, managers must recognize that responses that make sense in lodgepole pine forests may be ineffective, or even counterproductive and detrimental, in whitebark pine forests.

Raising the plight of this important ecosystem in the public consciousness has been an important contribution of our work. Whitebark pine loss in the GYE has not received the attention of the general public largely because it is not a commercial species, due to a lack of timber value, and because of the habitats it occupies, which typically are among the highest, most rugged, and most remote habitats on the continent. It is below the public's radar screen simply because most people do not venture into these places. Of the >.5 million visitors to Yellowstone National Park in 2010, only 6902 back-country permits (required for backcountry camping) were issued, involving 20 105 visitors, or ~0.5% of all visitors. Though this number does not tell us the exact number of people who venture into Yellowstone's whitebark pine habitat each year, it gives us some indication of the proportion of visitors who explore the more remote regions where the park's whitebark pine is located. Even for those visitors that do experience whitebark pine forests, few may recognize the reasons behind the devastation. Many visitors mistakenly assume fire to be the culprit, due to the immense and long-lasting public education program revolving around the 1988 fires. When compared to the 1988 fires, the area severely impacted by MPB in whitebark pine (~416 000 ha) already nearly equals the total area that was impacted by the 1988 Yellowstone fires (445 000 ha) ecosystem wide. Additionally, much of the 1988 fires burned in lodgepole pine forests that are supremely adapted to large-scale fire disturbance. The ecological impact of MPB in whitebark is a vastly different phenomenon that has the potential for regime shift in a sensitive and important ecosystem (Logan et al. 2010). Information provided by our LAS work highlights these massive impacts, potentially keeping whitebark pine forests from becoming another of the "places that no one knew," and perhaps even more optimistically, spurring action to formulate a truly strategic, systems-level management response.

Literature Cited

Amman, G. D. 1973. Population changes of the mountain pine beetle in relation to elevation. Environmental Entomology 2:541–547.

Bockino, N. K., and D. B. Tinker. 2012. Interactions of white pine blister rust and mountain pine beetle in whitebark pine ecosystems in the Southern Greater Yellowstone Area. Natural Areas Journal 32:31–40.

Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains. Oikos 82:561–573.

Ciesla, W. M., and M. M. Furniss. 1975. Idaho's haunted forests. American Forests 81:32–35.

Congalton, R. G. 1991. A review of assessing the accuracy of classification of remotely sensed data. Remote Sensing of Environment 37:35–56.

Coops, N. C., M. Johnson, M. A. Wulder, and J. C. White. 2006. Assessment of QuickBird high spatial resolution imagery to detect red attack damage due to mountain pine beetle infestation. Remote Sensing of Environment 103:67–80.

Dennison, P. E., A. R. Brunelle, and V. A. Carter. 2010. Assessing canopy mortality during a mountain pine beetle outbreak using GeoEye-1 high spatial resolution satellite data. Remote Sensing of Environment 114:2431–2435.

Despain, D. G. 1990. High-mountain resources of National Park Service lands. Page 386 in W. Schmidt and K. J. MacDonald, editors. Proceedings-symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989; Bozeman, Montana. General Technical Report INT-270. USDA Forest Service, Intermountain Research Station Ogden, Utah, USA.

Ellison, A. M., et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forest ecosystems. Frontiers in Ecology and the Environment 3:479–486.

ESRI. 2009. ArcGIS version 9.3. ESRI, Redlands, California, USA.

Farnes, P. E. 1989. SNOTEL and snow course data describing the hydrology of whitebark pine ecosystems. Pages 302–304 in W. Schmidt and K. J. MacDonald, editors. Proceedings-symposium on whitebark pine ecosystems: ecology and

management of a high-mountain resource; 1989; Bozeman, Montana. General Technical Report INT-270. USDA Forest Service, Intermountain Research Station Ogden, Utah, USA.

Franklin, S. E., M. A. Wulder, R. S. Skakun, and A. L. Carroll. 2003. Mountain pine beetle red-attack forest damage classification using stratified Landsat TM data in British Columbia, Canada. Photogrammetric Engineering and Remote Sensing 69:283–288.

Gibson, K., K. Skov, S. Kegley, C. Jorgensen, S. Smith, and J. Witcosky. 2008. Mountain pine beetle impacts in high-elevation five-needle pines: Current trends and challenges. Forest Health Protection R1–08-020. USDA Forest Service, Northern Region, Missoula, Montana, USA.

Goetz, W., P. Maus, and E. Nielsen. 2009. Mapping whitebark pine canopy mortality in the Greater Yellowstone Area. RSAC-0104RPt1. USDA Forest Service, Remote Sensing Application Center, Salt Lake City, Utah, USA.

Hicke, J. A., and J. A. Logan. 2009. Mapping whitebark pine mortality caused by a mountain pine beetle outbreak with high spatial resolution satellite imagery. International Journal of Remote Sensing 30:4427–4441.

Holmes, G. W., and J. H. Moss. 1955. Pleistocene geology of the southwestern Wind River Mountains, Wyoming. Bulletin of the Geological Society of America 66:629–664.

Jewett, J. T., R. L. Lawrence, L. A. Marshall, P. E. Gessler, S. L. Powell, and S. L. Savage. 2011. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. Forest Science 57:320–335.

Keiter, R. B., and M. S. Boyce. 1991. The Greater Yellowstone Ecosystem, redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. International Conference on Bear Research and Management 5:166–173.

Kendall, K. C., and S. F. Arno. 1990. Whitebark pine: an important but endangered wildlife resource. Pages 264–273 in W. Schmidt and K. J. MacDonald, editors. Proceedings-symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989; Bozeman, Montana. General Technical Report INT-270. USDA Forest Service, Intermountain Research Station Ogden, Utah, USA.

Landenburger, L., R. L. Lawrence, S. Podruzny, and C. C. Schwartz. 2008. Mapping regional distribution of a single tree species: whitebark pine in the Greater Yellowstone Ecosystem. Sensors 8:4983–4994.

Landis, J. R., and G. G. Koch. 1977. The measurement of observer agreement for categorical data. Biometrics 33:613–619.

Lillesand, T. W., and R. W. Kiefer. 1994. Remote sensing and image interpretation. Wiley, New York, New York.

Locke, W. W. 1989. Present climate and glaciation of Western Montana, U.S.A. Arctic and Alpine Research 21(17):234–244.

Logan, J. A., and W. W. Macfarlane. 2010. Beetle devastates Yellowstone whitebark pine forests. ActionBioscience American Institute of Biological Sciences, Washington, D.C., USA. http://www.actionbioscience.org/environment/loganmacfarlane.html

Logan, J. A., W. W. Macfarlane, and L. Willcox. 2009. Effective monitoring as a basis for adaptive management: a case history of mountain pine beetle in Greater Yellowstone Ecosystem whitebark pine. iForest 2:19–22.

Logan, J. A., W. W. Macfarlane, and L. Willcox. 2010. Whitebark pine vulnerability to climate change induced mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications 20:895–902.

Logan, J. A., and J. A. Powell. 2004. Modeling mountain pine beetle phenological response to temperature. Pages 210–222 in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Mountain pine beetle symposium: challenges and solutions,

October 30–31, 2003, Kelowna, British Columbia, Canada. Information Report BC-X-399. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.

Lorenz, T. J., C. Aubry, and R. Shoal. 2008. A review of the literature on seed fate in whitebark pine and the life history traits of Clark's nutcracker and pine squirrels. General Technical Report PNW-GTR-742. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Marston, R. A., and J. E. Anderson. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. Conservation Biology 5:338–346.

Mattson, D. J., and D. P. Reinhart. 1994. Bear use of whitebark pine seeds in North America. Pages 212–220 in W. C. Schmidt and F. K. Holtmeier, editors. Proceedings of the international workshop on subalpine stone pines and their environment: the status of our knowledge. General Technical Report INT-GTR-309. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.

McCaughey, W. W., and D. F. Tomback. 2001. The natural regeneration process. Pages 89–104 in D. F. Tomback, S. F. Arno, R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

McConnell, T. J., E. W. Johnson, and B. Burns. 2000. A guide to conducting aerial sketchmapping surveys. Report number FHTET 00-01. USDA Forest Service, Forest Health Technology Enterprise Team, Fort Collins, Colorado, USA.

McKinney, S. T., C. E. Fiedler, and D. F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications 19:597–607.

Meddens, A. J. H., J. A. Hicke, and L. A. Vierling. 2011. Evaluating the potential of multispectral imagery to map multiple stages of tree mortality. Remote Sensing of Environment 115:1632–1642.

Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier. 2005. Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society 86:39–49.

Perkins, D. L., and T. W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. Canadian Journal Forest Research 26:2123–2133.

Podruzny, S. R., D. P. Reinhart, and D. J. Mattson. 1999. Fire, red squirrels, whitebark pine, and Yellowstone grizzly bears. Ursus 11:131–138.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58:501–517.

Renkin, R. A., and D. G. Despain. 1992. Fuel moisture, forest type, and lightning-caused fire in Yellowstone National Park. Canadian Journal of Forestry Research 22:37–45.

Resler, L. M., and D. F. Tomback. 2008. Blister rust prevalence in krummholz whitebark pine: implications for treeline dynamics, Northern Rocky Mountains, Montana, U.S.A. Arctic, Antarctic, and Alpine Research 40:161–170.

Romme, W. H., M. S. Boyce, R. Gresswell, E. H. Merrill, G. W. Minshall, C. Whitlock, and M. G. Turner. 2011. Twenty years after the 1988 Yellowstone fires: Lessons about disturbance and ecosystems. Ecosystems 14: 1196–1215.

Schwandt, J., and S. Kegley. 2008. Whitebark pine stand conditions after mountain pine beetle outbreaks. USDA Forest Service, Northern Region, Missoula, Montana, USA. http://fhm.fs.fed.us/em/funded/08/int_em_08_02.pdf

Six, D. L., and J. C. Adams. 2007. Relationships between white pine blister rust and the selection of individual whitebark pine by the mountain pine beetle. Journal of Entomological Science 42:345–353.

Skakun, R. S., M. A. Wulder, and S. E. Franklin. 2003. Sensitivity of the thematic mapper enhanced wetness difference index to detect mountain pine beetle red-attack damage. Remote Sensing of Environment 86:433–443.

Thompson, D. R. 2009. Glacier variability (1966–2006) in the Wind River Range, Wyoming, U.S.A. Thesis. University of Wyoming, Laramie, Wyoming, USA.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird 16:123–161.

Tomback, D. F., S. F. Arno, and R. E. Keane. 2001. The compelling case for management intervention. Pages 4–25 in D. F. Tomback, S. F. Arno, R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Turiano, T. 2003. Select peaks of Greater Yellowstone. Indomitus Books, Jackson, Wyoming, USA.

U.S. Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list *pinus albicaulis* as endangered or threatened with critical habitat. Pages 42631–42654 in Federal Register, Volume 76, Number 138. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA. http://www. regulations.gov/#!documentDetail;D=FWS-R6-ES-2010-0047-0021

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increases Western U.S. forest wildfire activity. Science 313:940–943.

White, J. C., M. A. Wulder, D. Brooks, R. Reich, and R. D. Wheate. 2005. Detection of red attack stage mountain pine beetle infestation with high spatial resolution satellite imagery. Remote Sensing of Environment 96:340–351.

Wulder, M. A., C. C. Dymond, J. C. White, D. G. Leckie, and A. L. Carroll. 2006a. Surveying mountain pine beetle damage of forests: A review of remote sensing opportunities. Forest Ecology and Management 221:27–41.

Wulder, M. A., J. C. White, B. Bentz, M. F. Alvarez, and N. C. Coops. 2006b. Estimating the probability of mountain pine beetle red-attack damage. Remote Sensing of Environment 101:150–166.

Wulder, M. A., J. C. White, N. C. Coops, and C. R. Butson. 2008. Multi-temporal analysis of high spatial resolution imagery for disturbance monitoring. Remote Sensing of Environment 112:2729–2740.

Supplemental Material

Appendix A

Figure showing Greater Yellowstone Ecosystem (GYE) whitebark pine distribution contained in either national parks or designated wilderness (*Ecological Archives* A023-021-A1).

Appendix B

Figure showing 2009 LAS flight lines (*Ecological Archives* A023-021-A2).

Appendix C

Figure delineating catchment boundary within mountainous region of the GYE (*Ecological Archives* A023-021-A3).

Appendix D

Mountain pine beetle-caused mortality rating system (*Ecological Archives* A023-021-A4).

Appendix E

GYE-wide whitebark pine catchment map (*Ecological Archives* A023-021-A5).

Appendix F

Figure showing whitebark pine mortality ground verification (*Ecological Archives* A023-021-A6).

Appendix G

Figure showing aspect-related mortality pattern (*Ecological Archives* A023-021-A7).

Appendix H

Figure showing mid-slope mortality pattern (*Ecological Archives* A023-021-A8).

Supplement

Google Earth file (.kml) containing a "pop-up" aerial oblique image and numeric (0–5.4) mortality rating based on the mountain pine beetle mortality (MPBM) rating system for all "look-at points" used and referenced in this study (see Fig. 5 in main text) (*Ecological Archives* A023-021-S1).