

Utah State University

DigitalCommons@USU

The Bark Beetles, Fuels, and Fire Bibliography

Quinney Natural Resources Research Library,
S.J. and Jessie E.

4-14-2016

Recent Tree Mortality in the Western United States from Bark Beetles and Forest Fires

Jeffrey A. Hicke

Arjan J. H. Meddens

Crystal A. Kolden

Follow this and additional works at: <https://digitalcommons.usu.edu/barkbeetles>



Part of the [Ecology and Evolutionary Biology Commons](#), [Entomology Commons](#), [Forest Biology Commons](#), [Forest Management Commons](#), and the [Wood Science and Pulp, Paper Technology Commons](#)

Recommended Citation

Jeffrey A.; Hick; Arjan J. H., Meddens; Kolden, Crystal. 2016. Recent Tree Mortality in the Western United States from Bark Beetles and Forest Fires. *Forest Science* 62(2): 141-153.

This Article is brought to you for free and open access by the Quinney Natural Resources Research Library, S.J. and Jessie E. at DigitalCommons@USU. It has been accepted for inclusion in The Bark Beetles, Fuels, and Fire Bibliography by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



forest ecology

Recent Tree Mortality in the Western United States from Bark Beetles and Forest Fires

Jeffrey A. Hicke, Arjan J.H. Meddens, and Crystal A. Kolden

Forests are substantially influenced by disturbances, and therefore accurate information about the location, timing, and magnitude of disturbances is important for understanding effects. In the western United States, the two major disturbance agents that kill trees are wildfire and bark beetle outbreaks. Our objective was to quantify mortality area (canopy area of killed trees), which better represents impacts than affected area (by beetles) or burn perimeter area, and characterize patterns in space and time. We based our estimates on aerial surveys for bark beetles and the Monitoring Trends in Burn Severity database (from satellite imagery) for fires. We found that during the last three decades, bark beetle-caused mortality area was 6.6 Mha (range of estimates, 0.64–7.8 Mha; 7.1% [0.7–8.4%] of the forested area in the western United States) and fire-caused mortality area was 2.7–5.9 Mha (2.9–6.3%). Mortality area from beetles and fire was similar to recent harvest area from a national report. Although large outbreaks and fires occurred before 2000, substantially more trees were killed since then. In several forest types, mortality area exceeded 20% of the total forest type area. Our mortality area estimates allow for comparisons among disturbance types and improved assessment of the effects of tree mortality.

Keywords: forest disturbances, Monitoring Trends in Burn Severity, aerial surveys

Disturbances that kill trees are important processes that greatly influence forests (Anderegg et al. 2013). Stand structure and function are altered after such disturbances, sometimes dramatically (Swanson et al. 2010, Larson and Churchill 2012). Stand age distributions are modified, and tree species composition may be affected (Veblen et al. 1991, Lutz et al. 2012). Wildlife habitat is influenced through decreased forest cover and increased number of snags (Hutto 1995, Saab et al. 2014). Tree mortality modifies carbon stocks (Hicke et al. 2013), and the reduction in photosynthesis and increase in decomposition after tree mortality can result in a substantial reduction in carbon sequestration (Hicke et al. 2012a, Earles et al. 2014). Water quantity is affected through lower transpiration and snow interception by the canopy, which result in alterations to snowpack and streamflow, and water quality is affected by increased erosion and sedimentation (Robichaud 2000, Pugh and Gordon 2012, Harpold et al. 2013) and changes in chemical composition (Mikkelsen et al. 2013). Direct human uses of disturbed forests are influenced through altera-

tions to timber yield (both increases and decreases, depending on timing and situation) and recreational activities and infrastructure affected by falling trees (Weed et al. 2013).

Globally, tree mortality from drought and biotic agents appears to be increasing, driven in part by climate change (van Mantgem et al. 2009, Allen et al. 2010, Weed et al. 2013). In some regions such as the western United States, wildfires have been more frequent in recent decades in response to warmer and drier conditions (Westerling et al. 2006). Given continued warming in the future, theoretical understanding and modeling have suggested continued tree mortality in the coming years from insects (Hicke et al. 2006, Bentz et al. 2010), hotter droughts (Williams et al. 2013, Allen et al. 2015), and wildfires (National Research Council 2011).

Wildfire and insect outbreaks are the two major natural disturbances of forests in the western United States. Both of these disturbance types are strongly coupled to climate (Pyne et al. 1996, Bentz et al. 2010), and warming and drought in recent decades have probably influenced the extent and severity of tree mortality from fires

Manuscript received July 14, 2015; accepted October 8, 2015; published online November 19, 2015.

Affiliations: Jeffrey A. Hicke (jhicke@uidaho.edu), Department of Geography, University of Idaho, Moscow, ID. Arjan J.H. Meddens (ameddens@uidaho.edu), University of Idaho. Crystal A. Kolden (ckolden@uidaho.edu), University of Idaho.

Acknowledgments: Support was provided by the US Geological Survey's Ecosystems and Climate and Land Use Change mission areas (through the US Geological Service Western Mountain Initiative project, Award G09AC00337), the Los Alamos National Laboratory (Subcontract 193703-1), the National Oceanic and Atmospheric Administration (NOAA) (Award NA09OAR4310194), the National Science Foundation (Award Number EAR-0910928), the USDA Forest Service Western Wildland Environmental Threat Assessment Center (Agreement PNW-08-JV-1126900-082), NASA (Agreement NNX11AO24G S03), and the Agriculture and Food Research Initiative of the USDA National Institute of Food and Agriculture (Grant 2013-67003-20652). We thank Benjamin C. Bright for help with the processing of the 2011 and 2012 aerial survey data. We also thank the anonymous reviewers and associate editor, whose comments improved the article. Lastly, we thank Craig D. Allen, USGS, for assistance, and Benjamin C. Bright for help with the processing of the 2011 and 2012 aerial survey data.

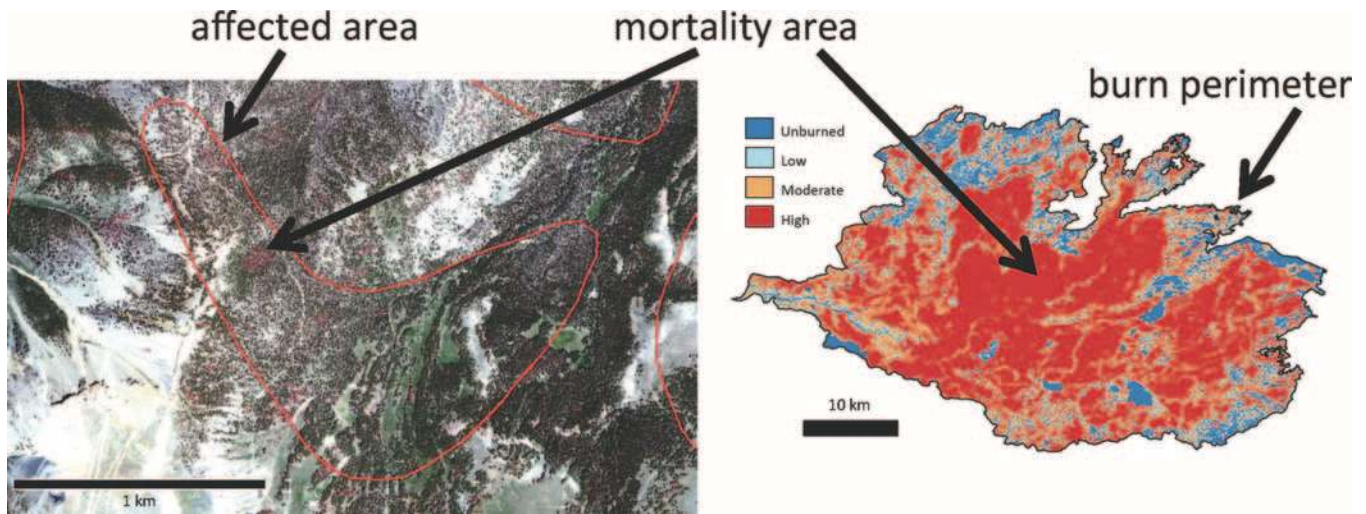


Figure 1. Illustrations of affected area versus mortality area for bark beetles (left) and burn perimeter versus mortality area for forest fires (right). Left: QuickBird satellite image in 2005 near Railroad Ridge, Idaho (killed trees are red in this true-color image) with red polygons showing mountain pine beetle-caused whitebark pine affected area as reported by 2005 USDA Forest Service ADSs. Right: Burn perimeter and burn severity classes (unburned, dark blue; low, light blue; moderate, orange; high, red) from MTBS for the 2013 Rim Fire in California (classification thresholds from Miller et al. 2009); in this study, we associate tree mortality with high or moderate+high classes.

and insects (Dale et al. 2001, Williams et al. 2013). These disturbances can range from low severity and limited spatial extent (e.g., 1 year of defoliation, endemic populations of mountain pine beetle [*Dendroctonus ponderosae* Hopkins], or low-intensity surface fire) to high severity over large areas (e.g., mountain pine beetle outbreaks [Meddens and Hicke 2014] or widespread crown fires [Turner et al. 2003, Stephens et al. 2014]). Impacts to forests clearly differ between these two extremes (Miller et al. 2009). In this study, we focus on tree mortality because of its substantial effects on forest ecosystems.

Quantifying tree mortality from fires and insect outbreaks is critical for increasing the understanding of the magnitude and causes of these events as well as for evaluating their impacts. Past reports of the extent of these disturbances have relied on burn perimeters for fires and affected areas for beetle outbreaks. However, these area metrics include both killed and live trees. Burn perimeters include lower severity and/or unburned areas within a fire (Kolden et al. 2012), and affected areas of beetle outbreaks are the areas of polygons drawn by observers in airplanes to record damage and include many live trees (US Department of Agriculture [USDA] Forest Service 2005) (Figure 1). Therefore, these metrics overestimate the actual area of tree mortality. Furthermore, although changes in time and space of burn perimeters or affected area provide indices of fire and biotic activity, comparisons of the extent of tree mortality among disturbance agents (e.g., biotic, fires, drought, and harvest) using these data are challenging because of the different metrics. As a result of these challenges, no study to date has developed detailed estimates of the extent of tree mortality, accounting for only killed trees, from bark beetles and fires across larger regions such as the western United States.

Our objectives in this study were to quantify the canopy area of trees killed by forest fires and bark beetles in the western United States. We refer to this canopy area as “mortality area.” We used satellite-derived burn severity maps and aerial surveys of bark beetle damage to estimate mortality area during the last several decades and compared this to burn perimeter area and affected area. We characterized the spatial and temporal patterns of mortality area using ancillary data sets that allowed us to document patterns among

forest types, land ownerships, and protected area status. We compared tree mortality between these two disturbance agents and with published harvest area. Finally, given interest in the extent to which wildfires follow bark beetle outbreaks (Hicke et al. 2012b), we describe preliminary analyses of this overlap. Previous work characterized tree mortality from bark beetles and fire in the western United States in terms of carbon (Hicke et al. 2013). In this study, we quantified area of mortality because of the broader applicability of mortality area to forest scientists and managers. In addition, we updated databases to 2012 and include more analyses of these natural disturbances.

Methods

We used two recently developed data sets to estimate the amount of mortality area (canopy area of killed trees) from forest fires and bark beetle outbreaks. We focused on the western United States where recent data sets have been developed to map burn severity in large fires and tree mortality from bark beetles.

Fire-Caused Tree Mortality

Two estimates (lower and upper) of tree mortality from wildfires were produced from the Monitoring Trends in Burn Severity (MTBS) database for 1984–2012 (Eidenshink et al. 2007) (Figure 2). In the western United States, MTBS maps fires of >405 ha (1,000 acres). Fires greater than this size threshold constitute 95% of the total burned area in this region (Zhu and Eidenshink 2007) and, in some areas that experience primarily stand-replacing fire, greater than 95% (Kolden et al. 2012). This data set was developed using 30-m Landsat imagery, and fires are reported with annual resolution. MTBS uses the differenced normalized burn ratio (dNBR), a bitemporal spectral index (pre- and postfire), as a proxy for burn severity, which has been field validated (Key and Benson 2006, Zhu et al. 2006). Thresholds to differentiate low, moderate, and high burn severity were set subjectively by MTBS analysts (Eidenshink et al. 2007). Here we assume that higher burn severity is associated with tree mortality. However, which classes correspond to mortality

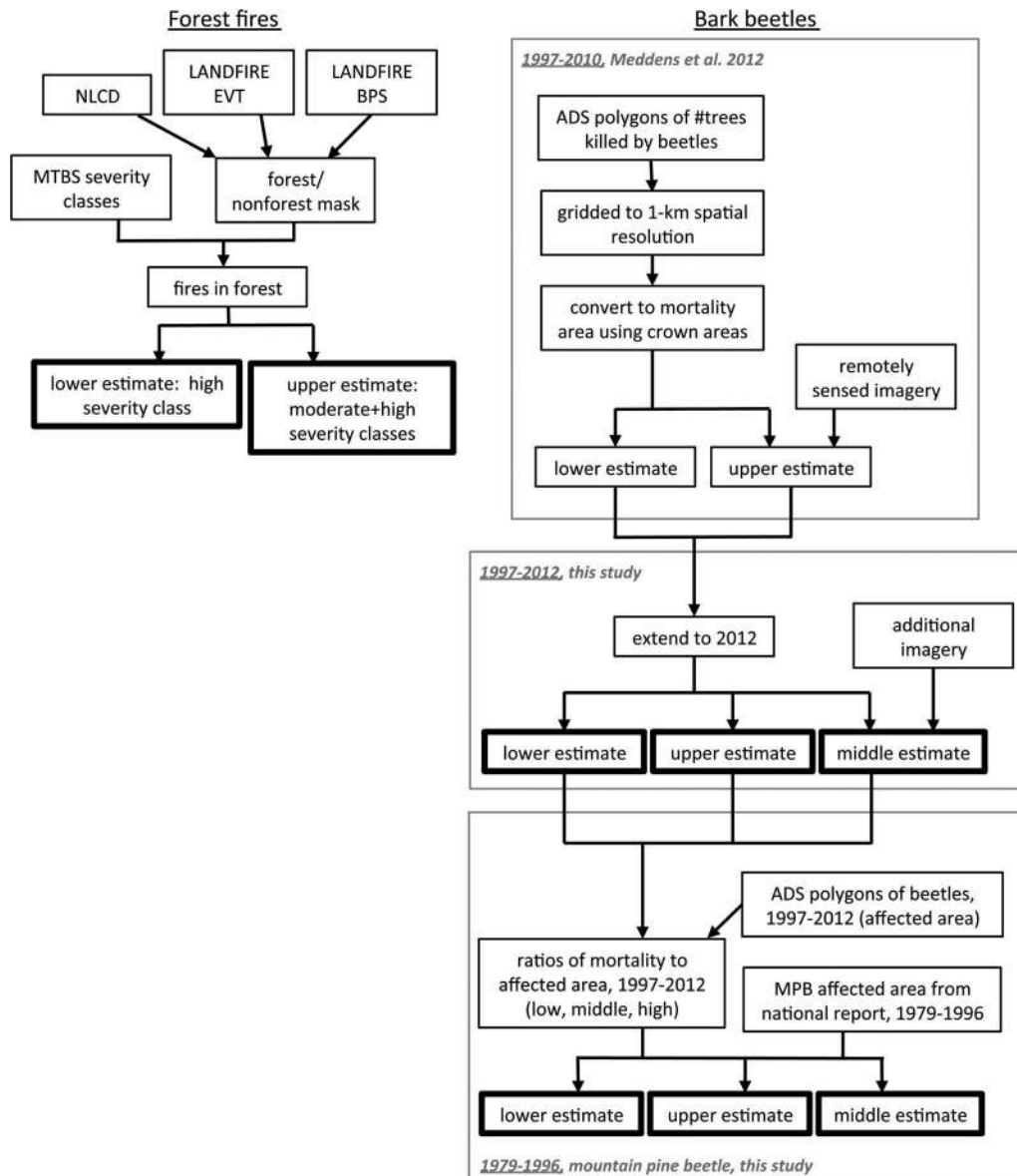


Figure 2. Flow diagram showing processing steps for computing tree mortality area from forest fires and bark beetles. Boxes with thick lines indicate products of this study: wildfire-caused mortality area, 1984–2012 (left); spatially explicit beetle-caused mortality area, 1997–2012 (middle right); regional mountain pine beetle (MPB)-caused mortality area, 1979–1996 (lower right). See text for definitions, acronyms, and citations.

is subject to some uncertainty (Kolden et al. 2015). As a result, we provide two estimates of fire-caused mortality. We chose the high-severity class for the lower estimate and summed the moderate- and high-severity (moderate+high severity) classes for our upper estimate. A previous review of published studies suggested good representation of tree mortality by using both moderate- and high-severity fires (Ghimire et al. 2012).

We downloaded 30-m maps of annual burn severity from the MTBS website.¹ We masked out nonforest areas by developing a forest/nonforest map from several data sets that quantify forest (canopy) cover. We identified forest classes in the US Geological Survey National Land Cover Dataset (NLCD 2001, version 2.0) (Homer et al. 2004) and the LANDFIRE Existing Vegetation Types (EVT) data set using the 2008 Refresh version (Rollins 2009). We combined these maps with a union operation; i.e., a grid cell classified as forest in either data set was identified as forest. Because we noted

that some recent disturbances were misclassified as nonforest, we added forest locations from the LANDFIRE Biophysical Settings (BpS) map (Rollins 2009) except in areas where the EVT data set mapped agriculture. The BpS map was produced by LANDFIRE by modeling potential vegetation. The resulting 30-m forest/nonforest mask was applied to the MTBS burn severity maps. We then aggregated the 30-m forest fire mortality area (assuming complete mortality at the 30-m resolution) to 1-km resolution to match the bark beetle data set to produce a percentage (or equivalently, hectares) of mortality within a 1-km grid cell.

On May 31, 2003, the Landsat 7 ETM+ instrument experienced a Scan Line Corrector (SLC) failure, which led to spatially incomplete imagery thereafter (Markham et al. 2004). Because some of the MTBS burn severity data used ETM+ imagery and because the spatial gaps are identified as a separate class in the MTBS database within fire perimeters, we estimated the effect of this loss

on mortality area (but did not modify our estimates). To accomplish this, we first calculated the ratio of regionwide (summed) area of moderate+high burn severity to the area of all unburned and burned classes for each year. We then multiplied these ratios by the area of “nonprocessing area mask” (gaps caused by the SLC failure and, to some degree, cloud cover) to estimate the mortality area missed by these gaps. Our assumption was that burn severities occur at the same proportions within these gaps, which are regularly spaced across the landscape, as outside the gaps. We found that these estimates of the “hidden” area of tree mortality (associated with “nonprocessing”) was 0.2–8.6% (annual values for the period 2003–2012) of the mortality area from the recorded moderate+high burn severity, with a mean of 3.3%. Thus, our calculations suggest that we underestimate mortality area somewhat because of the SLC error.

Beetle-Caused Tree Mortality

We updated a data set produced by Meddens et al. (2012) to estimate the mortality area from bark beetle attack (Figure 2). This data set was initially developed using USDA Forest Service Aerial Detection Surveys (ADSs) in 1997–2010. Full details are provided in Meddens et al. (2012); here, we briefly summarize the methods. Meddens et al. (2012) gridded the polygons with the number of trees killed by bark beetles reported by aerial surveys to 1-km spatial resolution and then estimated mortality area by multiplying this number of trees killed by species-specific crown areas. The authors reported two estimates. The first (lower) estimate was computed using the original values for number of trees killed included in the aerial survey database. Because underestimation has been recognized by multiple authors using various means (Meigs et al. 2011, Meddens et al. 2012), Meddens et al. (2012) also developed an upper estimate. This upper estimate was produced by comparing the lower estimate with mortality area calculated using high-resolution remotely sensed imagery in three different locations and forest types. Three resulting adjustment factors forced a match of the aerial survey-based mortality area to the remotely sensed-based mortality area. The authors calculated a lower factor for piñon pines (*Pinus edulis* Engelm. and *Pinus monophylla* Torr. & Frém.), a higher factor for lodgepole pines (*Pinus contorta* Dougl.), and an intermediate factor developed from whitebark pines (*Pinus albicaulis* Engelm.) and used for all other tree species.

Since Meddens et al. (2012), we added 2 years of data (2011–2012). We also analyzed additional remotely sensed imagery together with aerial surveys in lodgepole pine forests and found that the mean of adjustment factors from these analyses was close to the intermediate adjustment factor (originally developed in whitebark pine locations) reported in Meddens et al. (2012). Therefore, we created a middle estimate of mortality area that differs from the upper estimate in that we applied the intermediate adjustment factor from Meddens et al. (2012) to lodgepole pines instead of the upper adjustment factor (as described in Hicke et al. 2013). Because the middle estimate was produced using fine-resolution aerial and satellite imagery that were developed with high accuracy and based on comparisons with field data and bark beetle information from British Columbia, we consider the middle estimate to be most realistic of the three. However, we note that uncertainties about the actual mortality area remain because our comparisons were limited in space and time and because the aerial surveys are subjective in nature and conducted by multiple observers. Bark beetle-caused mortality area reported here corresponds to the year of detection,

which for many tree species is about 1 year after beetle attack (Wulder et al. 2006, Clifford et al. 2008). We used this data set to separate mortality from different bark beetle species and to separate mortality of different tree species. Both attributes were recorded by aerial surveyors and stored in the ADS database.

To provide more information about earlier beetle infestations, we also estimated mortality area from affected area from mountain pine beetle outbreaks reported for the West back to 1979. This affected area is provided as an annual regional time series (USDA Forest Service 2004) and is not spatially explicit. We estimated the ratio of mortality area to affected area during 1997–2012 and then applied this ratio to the affected areas reported during 1979–1996. Because these results rely on this ratio and are not based on the observed number of killed trees and because we necessarily assume that the ratio remains constant in time, we suggest that these results should be viewed cautiously.

Characterization of Tree Mortality by Forest Type, Owner, and State

Three data sets permitted additional characterization of tree mortality. First, we stratified tree mortality by forest type by using the 2001 map of Rufenacht et al. (2008), which we aggregated from 250-m spatial resolution to 1 km. This data set maps existing forest types based on the USDA Forest Service plot network, satellite imagery, and other ancillary data. Second, we used characteristics of owner name (e.g., USDA Forest Service, National Park Service, private) and protected status from the US Protected Areas database (version 2.1), available at 30-m spatial resolution (Gergely and McKerrow 2013). (Although we recognize that the USDA Forest Service, for example, is not a landowner, here we follow the terminology of the Protected Areas database.) Protected status codes range from 1 to 4 and are based on conservation measures to protect and restore ecosystems. Status 1 lands are areas having permanent protection and are those with the highest amount of protection, such as national parks. Status 2 lands include wilderness areas and have permanent protection in place but allow some human modifications to the landscape that include disturbance, renewable resource use, and visitation. Status 3 lands have some protection but allow recreational or resource extraction activities and include national forestlands. Status 4 lands have no protection and are associated with private lands. We aggregated the forest type, owner name, and protected status maps to 1-km spatial resolution using the modal (plurality) class. Third, we include an analysis of mortality area by state. We stratified our time series of maps of tree mortality from fires and bark beetles by these forest attributes.

Wildfires after Beetle Outbreaks

We investigated areas that burned after bark beetle outbreaks in a preliminary way because the spatial resolution of the data sets (1 km) only allowed for coarse-level analysis. We chose percentage mortality thresholds of 50 and 75% (two separate analyses) to identify cells with fires after beetle outbreaks. That is, we classified grid cells as having beetle outbreaks or fire based on a threshold and then searched for grid cells that experienced fire after beetle-caused tree mortality. We chose the more conservative metric of percentage of mortality within a grid cell instead of percentage of mortality within the forested area of a grid cell to increase the likelihood of overlap between outbreaks and fire. We report regionwide cumulative statistics and inspected maps of overlap to identify fires that burned in areas with substantial amounts of beetle-caused tree mortality.

Table 1. Cumulative and annual mortality area for different disturbance types.

Disturbance type	Years	Cumulative mortality area ^a	Annual mean mortality area ^a
Bark beetles	1979–2012 ^b	6.6 Mha (0.64–7.8)	0.19 Mha/yr (0.019–0.23)
		7.1% (0.7–8.4)	0.21%/yr (0.02–0.25)
	1997–2012	5.2 Mha (0.53–6.1)	0.33 Mha/yr (0.03–0.38)
Forest fires		5.6% (0.57–6.5)	0.35%/yr (0.04–0.41)
	1984–2012	2.7–5.9 Mha	0.095–0.20 Mha/yr
		2.9–6.3%	0.10–0.22%/yr
Harvest (Smith et al. 2009)	1997–2012	2.1–4.5 Mha	0.12–0.27 Mha/yr
		2.3–4.8%	0.13–0.29%/yr
	2001–2005	NA	0.24 Mha/yr clearcut 0.33 Mha/yr partial cut

^a For bark beetles, the middle (most realistic) estimate is reported with the range from the lower and upper estimates in parentheses; for forest fires, the high and moderate+high severity estimates are reported. NA, not available.

^b 1979–1996 includes mountain pine beetle only, estimated from mortality area/affected area during 1997–2012 and affected area during 1979–1996.

Harvest Area

We compared mortality area from wildfires and bark beetles to harvest area. Annual harvest area by region was included in a report on forest resources in the United States in 2007 (Smith et al. 2009) (later national reports do not include harvest area). The harvest area is broken down by clearcut and partial cut. We summed the Rocky Mountain region and the Pacific Coast region for our comparison. The Pacific Coast region includes Alaska, yet the harvest area table does not provide information at finer spatial resolution. We assessed the contribution of Alaska by noting that the volume of roundwood products harvested there was 2.3% of that of the Pacific Coast region (Smith et al. 2009) and therefore assumed that the forest harvest area in Alaska was similarly minor.

We compared cumulative mortality area with burned perimeters and affected areas. Burn perimeters were summed using the MTBS database to identify the total fire-affected area. Affected area was computed from the ADS data sets by extracting polygons with bark beetle-caused tree mortality, overlaying polygons from all years (1997–2012) and summing this nonoverlapping area.

Results

For clarity and conciseness, we focus our discussion on the middle estimate of tree mortality for beetles, which we consider the most realistic, and the upper estimate for fire (moderate+high severity). However, given uncertainties in our estimates, we also present results for the other estimates (see Methods and Discussion for more information on uncertainties).

Regionwide Mortality Area

Cumulative mortality area from fires during 1984–2012 was 5.9 Mha or 6.3% of forested area in the western United States (Table 1). During 1997–2012, bark beetles caused 5.2 Mha of tree mortality (middle, most realistic estimate), corresponding to 5.6% of the forested area (for comparison, forest fires killed 4.5 Mha [upper estimate] of trees during this period). With inclusion of estimates from the earlier period (1979–1996), which are subject to greater uncertainty (see Methods and Discussion), bark beetle-caused mortality was 6.6 Mha (7.1% of the forested area).

The mean annual mortality area from beetles during 1997–2012 was higher than that from fire (0.33 versus 0.27 Mha/year, respectively). Harvest area during a similar period (2001–2005) was of

Table 2. Mortality area relative to affected area or burned perimeter.

Disturbance type	Years	Cumulative mortality area (Mha) ^{a,b}	Cumulative affected or burn perimeter area (Mha)	Percent mortality area ^{b,c}
Bark beetles	1997–2012	5.2 (0.53–6.1)	22.1	24 (2–28)
Forest fires	1984–2012	2.7–5.9	12.7	21–46
	1997–2012	2.1–4.5	9.7	20–44

^a From Table 1.

^b For bark beetles, the middle (most realistic) estimate is reported with the range from the lower and upper estimates in parentheses; for forest fires, the high and moderate+high severity estimates are reported.

^c Percent mortality area computed using cumulative mortality area and cumulative affected area (bark beetles) or burn perimeter area.

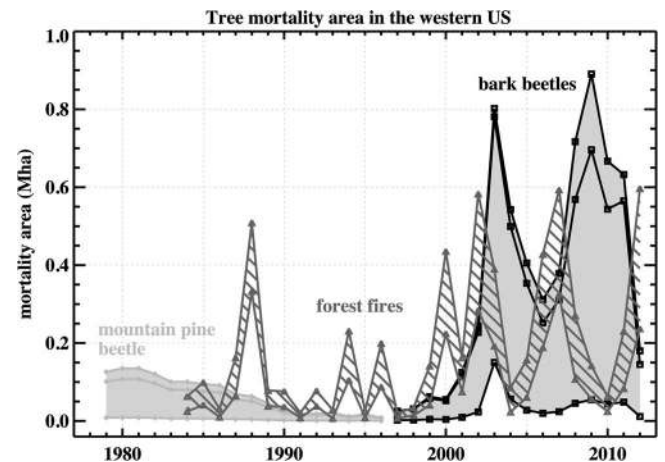


Figure 3. Cumulative tree mortality from bark beetles (black lines, lower, middle [most realistic], and upper estimates) and forest fires (gray lines and hatching, high, moderate+high severity) and an estimate of mountain pine beetle-caused mortality during 1979–1996 (light gray lines, lower, middle [most realistic], and upper estimates).

similar magnitude, with 0.24 Mha/year of clearcuts and 0.33 Mha/year of partial cuts (thinning) (Smith et al. 2009).

The importance of using mortality area versus affected area or burn perimeters for assessing extent of disturbance types and estimating impacts is illustrated by comparing these values (Table 2). The percentage of mortality area using moderate+high severity (less conservative estimate) was about 44–46% of the burn perimeter area (depending on the period considered), with that value decreasing to 20–21% if only high-severity areas (more conservative estimate) were considered. The middle estimate of mortality area from beetle outbreaks was 24% of affected area.

Timing of Mortality

Higher amounts of bark beetle-caused tree mortality occurred in several periods since 1980 (Figures 3 and 4). Mountain pine beetle outbreaks caused an average of 0.1 Mha of tree mortality annually in the early 1980s. Major outbreaks in this period were in southern Oregon, northwestern Montana, and the Greater Yellowstone Ecosystem (as indicated in, e.g., Williams and Birdsey 2003). In contrast to the period before 2000, in which mortality area was 0.05 Mha annually, the period beginning in 2000 experienced 0.32 Mha of mortality area per year. In the early 2000s, several species of bark beetles in combination with a severe drought killed trees across extensive areas. Ips beetles (*Ips confusus*) caused substantial tree mortality in the Southwest. Other tree species (from the ADS database)

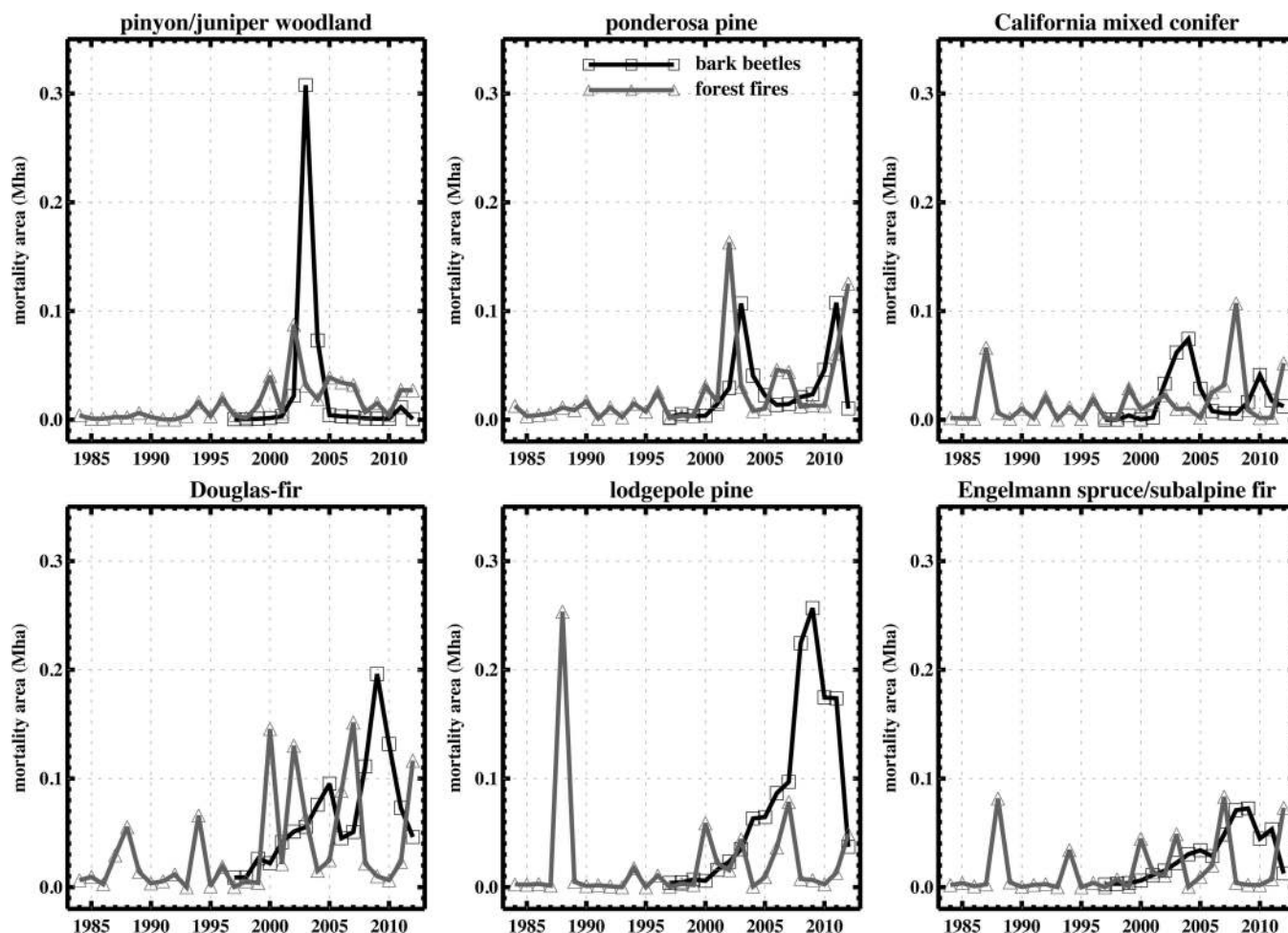


Figure 4. Bark beetle-caused tree mortality in 1997–2012 (black, middle estimate) and forest fire-caused tree mortality in 1984–2012 (gray, moderate+high severity) by forest type (derived from Ruefenacht et al. 2008). Note that forest type does not necessarily represent the killed tree species; in particular, lodgepole mortality from mountain pine beetle contributed to the higher values in Douglas-fir and Engelmann spruce/subalpine fir forest types from the late 2000s forward.

also experienced extensive mortality in the early 2000s, such as Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) attacked by Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopk.) and true firs (*Picea* spp.) and pines (*Pinus* spp.) attacked by engraver beetles (*Ips* spp.). The large amounts of mortality since 2008 were caused predominantly by multiple mountain pine beetle outbreaks throughout much of the western United States. Epidemics of this beetle species caused tree mortality primarily in lodgepole pine but also in whitebark pine, ponderosa pine (*Pinus ponderosa*), and other pine species. Bark beetle-caused tree mortality declined substantially in 2012, although mortality area was still about 0.15 Mha.

Forest fires caused lower tree mortality in the western United States than bark beetles. The peak years of mortality caused by fires were 1988, 2000, 2002, 2003, 2006, 2007, and 2012, in which about 0.45–0.6 Mha of trees were killed annually. Fires were less damaging to forests in earlier years of the study period, with only fires in 1988 causing substantial (0.5 Mha) mortality; annual average mortality area was 0.11 Mha/year before 2000. In contrast, mortality area has been notably higher since 2000 (0.32 Mha/year), but still less than that from bark beetles. Examples of extensive forest fires include those in the Greater Yellowstone Ecosystem in 1988 (lodgepole and Engelmann spruce [*Picea engelmannii* Parry]/subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] forest types), the Biscuit Fire in

southern Oregon and the Rodeo-Chediski Fire in Arizona in 2002 (both ponderosa pine forest type), and the Tripod Complex in northern Washington in 2007 (lodgepole pine forest type).

Mortality area from fires had high interannual variability, with many years of substantial tree mortality preceded and followed by years with low mortality. In contrast, bark beetles caused tree mortality within an outbreak location for multiple years. For example, field (Cole and Amman 1980) and remote sensing (Meddens and Hicke 2014) studies indicate that mountain pine beetles attack trees for 3–6 years or longer within a stand. Thus, the slower progression of beetle outbreaks reduced interannual variability in the mortality area time series.

Although the regional time series of mortality from fires and beetles might appear to show some interactions through temporal lags (Figure 3), it is important to recognize that disturbances that appear consecutive in time (e.g., fires in 2002 and bark beetles in 2003) did not overlap in space. Thus, Figure 3 by itself does not indicate interactions among these two disturbance agents.

Severity and Extent

Bark beetle outbreaks occurred in most forests of the western United States during 1997–2012 (Figure 5). Most locations with bark beetle activity experienced low amounts of mortality (low severity). However, substantial tree mortality at both a grid cell scale

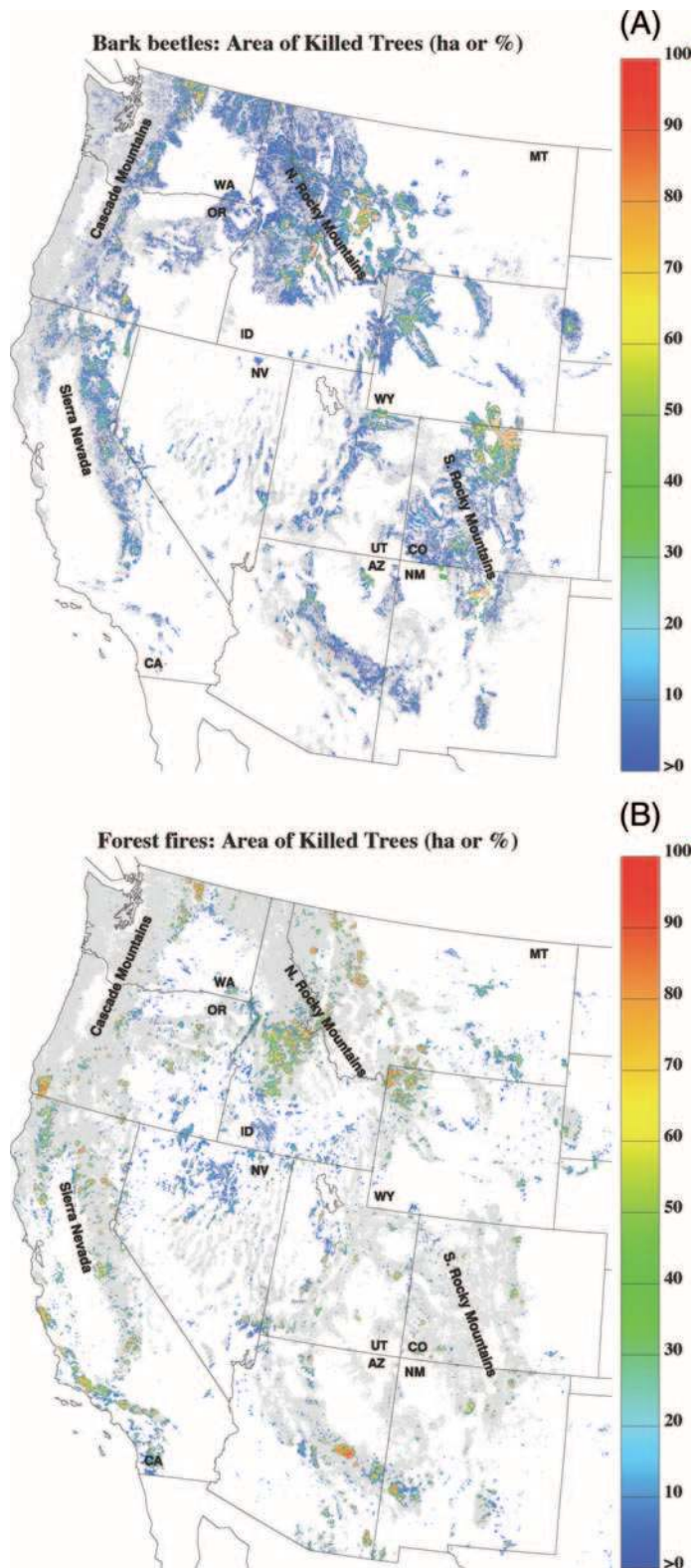


Figure 5. (A) Bark beetle-caused tree mortality, 1997–2012. (B) Forest fire-caused tree mortality, 1984–2012. Colors show numbers of hectares of tree mortality within each 1-km grid cell (which equals the percentage of the grid cell).

and aggregated over larger areas occurred in locations throughout the West. The forests on the Pacific Coast from northern California to northern Washington are notable for the lack of bark beetle activity.

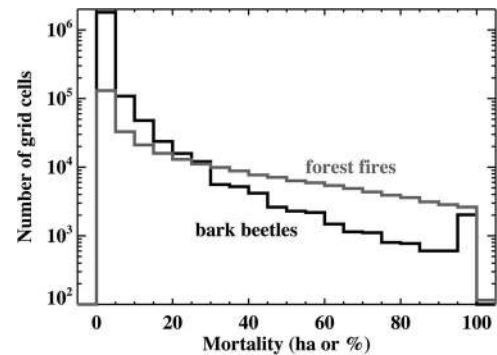


Figure 6. Distribution of percent mortality within 1-km grid cells (percentages of 1-km grid cells have same values as hectares) for bark beetles (black) and forest fires (gray). Only cells with some mortality are plotted. Bark beetles are a more diffuse disturbance agent, killing trees at lower percent mortality over larger areas than fires.

More localized tree mortality occurred from forest fires than from bark beetles (Figure 5). Fires had lower total spatial extent but higher severity (percentage mortality within a grid cell). In other words, fires occurred in fewer 1-km grid cells than beetle outbreaks (301,220 versus 2,047,491, respectively), but those grid cells that experienced fire had higher tree mortality on average (19.7% of a 1-km grid cell) than those grid cells that experienced beetle outbreaks (2.6%). Mortality from individual large fires (e.g., the Biscuit Fire in southern Oregon or the Yellowstone fires in northwest Wyoming) is clearly discernible. Central Idaho experienced both high tree mortality within fires as well as large burned area. Unlike for bark beetle outbreaks, most forested locations in the western United States have not experienced a tree-killing fire in recent decades.

Histograms of percentage mortality from fires and beetles within 1-km grid cells also support the differences in typical severity levels from these disturbance agents (Figure 6). Bark beetle outbreaks have many more cells with lower percent mortality than higher percent mortality (Figures 5 and 6). In contrast, although mortality area from fires is also higher at lower percent mortality than at higher percent mortality, a greater proportion of fires have higher percent mortality than bark beetle outbreaks.

Distribution of Mortality by Forest Type

Among forest types in the western United States, lodgepole pine forest type experienced the greatest mortality by bark beetles (Figure 7), and much of the mortality in the Douglas-fir forest type is from killed lodgepole pines (based on spatial comparison of the ADS-reported beetle species [mountain pine beetle] and the forest type map). Substantial mortality by bark beetles occurred in spruce-fir forest types because of western balsam bark beetles (*Dryocoetes confusus* [Swaine]) that attacked subalpine fir, mountain pine beetles that killed lodgepole pines, and spruce beetle (*Dendroctonus rufipennis* [Kirby]), which killed Engelmann spruce. Piñon pine mortality was comparable to that of other forest types in terms of absolute area but relatively lower when considered as a percentage of total area of piñon/juniper (*Juniperus* spp.) forest type. Mortality area from fires was greatest in ponderosa pine, lodgepole pine, Douglas-fir, and “nonforest” forest types. Although bark beetles caused mortality in ponderosa pine, piñon/juniper, California mixed conifer, and nonforest forest types, the amount of mortality caused by fire in these forest types was greater. The middle estimate of bark beetle-caused

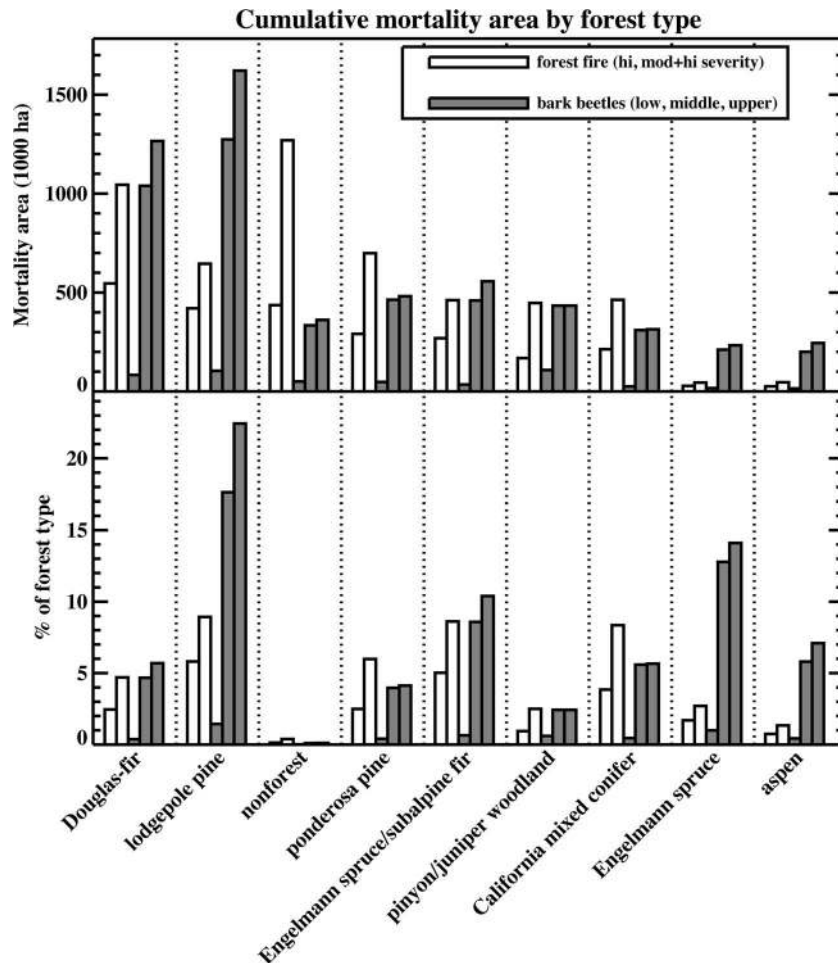


Figure 7. Cumulative bark beetle-caused tree mortality (1997–2012; gray, lower, middle [most realistic], and upper estimates) and forest fire-caused tree mortality (1984–2012; white, high and moderate+high severity) by forest type for (top) area (hectares) and (bottom) percentage of forest type (derived from Rufenacht et al. 2008). Note that forest type does not necessarily represent the killed tree species.

mortality exceeded that from forest fires in Douglas-fir, lodgepole pine, spruce, spruce-fir, and aspen forest types. The substantial area of forest fires classified as nonforest resulted from a mismatch in the different spatial resolutions of the forest type map (250 m) and the forest mask (30 m). The forest mask, used for selecting tree mortality areas, may have identified forest areas that occupied only a minor part of a 250-m forest type grid cell, which was classified as nonforest at the 250-m resolution. An additional possibility is that the forest mask and forest type maps were derived from imagery of different years and therefore different successional stages. A third possibility is related to the possibility of misclassification in one or both data sets. A large fraction of this nonforest area was in the coastal areas of southern California.

Distribution of Mortality by Landownership and Protected Status

The majority of these natural forest disturbances occurred on federal lands (10 Mha), with minor contributions from state, tribal, and private lands (each 1.4 Mha or less). The USDA Forest Service experienced the most mortality area by a substantial margin (almost 8 Mha, corresponding to 12% of Forest Service land) (Figure 8) as a result of the large area managed by the Forest Service coupled with high mortality. Other institutions had less than 1 Mha of mortality each. When considered as a percentage of total land, however, several institutions had mortality area that exceeded 2–3%. Significant

among these was the National Park Service, which experienced tree mortality from forest fires on 5% of its land.

Both forest fires and bark beetle outbreaks were concentrated on lands assigned a protected status of 3, which is associated with many national forests (Figure 9). Lower amounts of mortality area were associated with lands of other protected status. When considered as a percentage of total available land, Status 1 lands (most protected) experienced relatively high mortality from forest fires (7.5%). Bark beetle outbreaks killed trees on about 2–3% of lands with protected status 1–3 (having some level of protection).

Distribution of Mortality by State

Substantial variability in mortality area occurred among states (Figure 10). California had the largest mortality area from forest fires (1984–2012), over 1.3 Mha for the upper estimate. This amount exceeded any state-level bark beetle-caused mortality area, partially as a result of California also having the most extensive forest area. Idaho and Montana also had high tree mortality from fires. Colorado and Montana had the largest areas of bark beetle-caused mortality, at 1 and 0.9 Mha, respectively (based on the most realistic middle estimate and for 1997–2012). Many states had similar amounts of forest fire and beetle outbreaks, but two had substantial differences: California had greater fire-caused mortality area because of the large fires in the coastal mountains whose forests

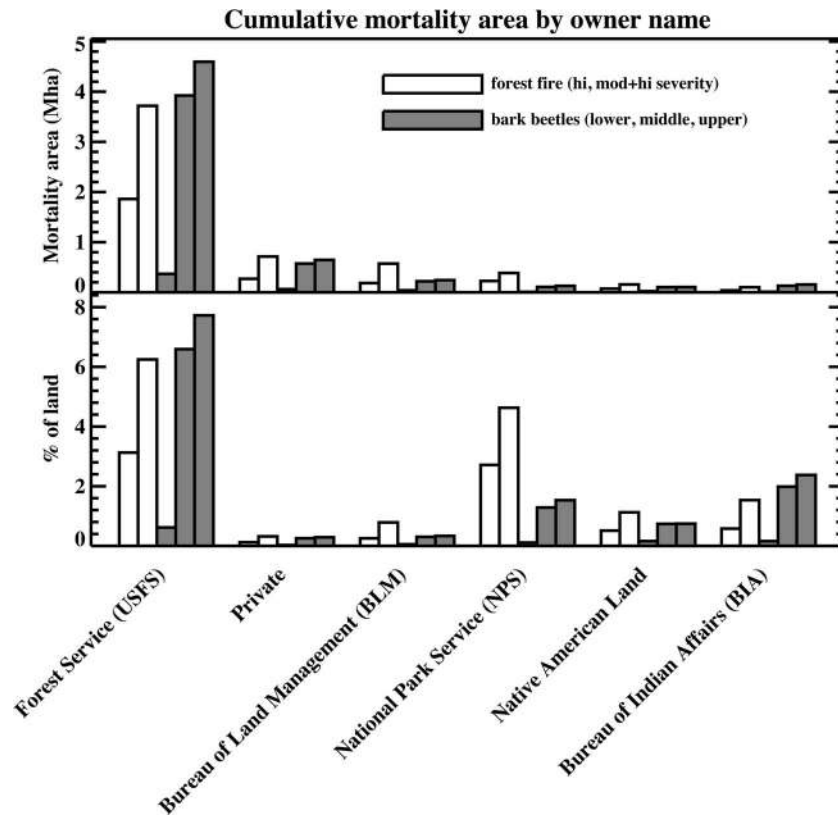


Figure 8. Cumulative bark beetle-caused tree mortality (1997–2012; gray, lower, middle [most realistic], and upper estimates) and forest fire-caused tree mortality (1984–2012; white, high and moderate+high severity) by owner name for (top) area (hectares) and (bottom) percentage of area.

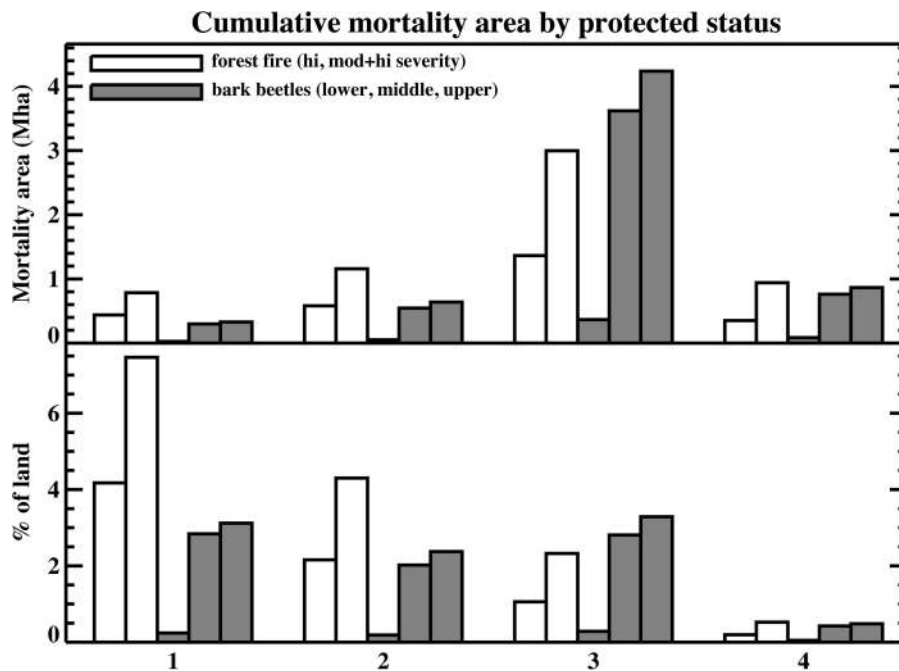


Figure 9. Cumulative bark beetle-caused tree mortality (1997–2012; gray, lower, middle [most realistic], and upper estimates) and forest fire-caused tree mortality (1984–2012; white, high and moderate+high severity) by protected status for (top) area (ha) and (bottom) percentage of area. Protected status ranges from highly protected (1) to no protection (4).

were not widely affected by bark beetles during the study period; and Colorado, which in this time period had particularly extensive and severe large beetle outbreaks but relatively fewer tree-killing forest fires.

Wildfires after Beetle Outbreaks

A 50% threshold for mortality area within a grid cell resulted in 74,562 ha of fire-caused mortality after bark beetle-caused mortality. This area represents 1.3% of the total mortality area from fires

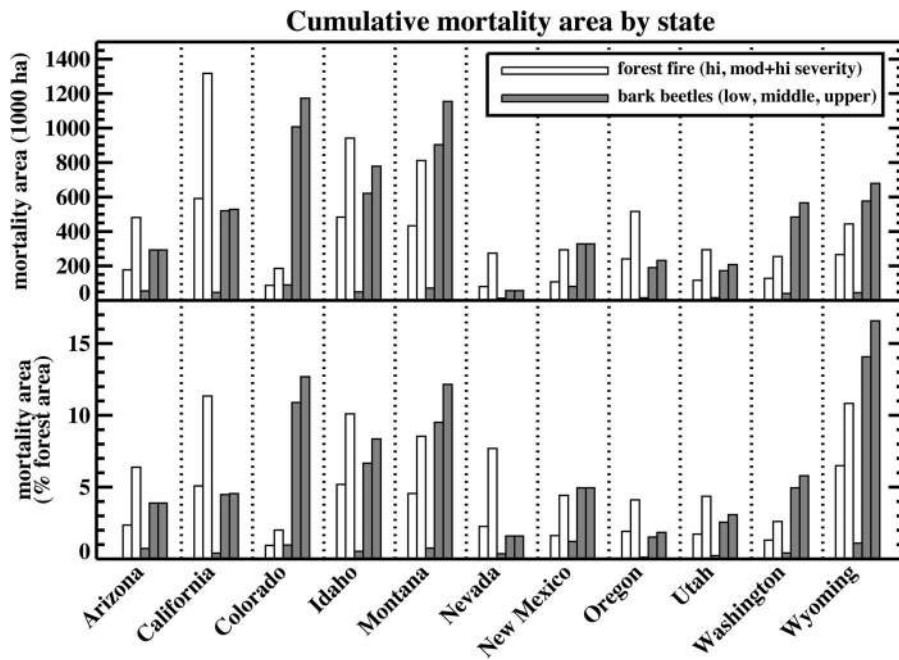


Figure 10. Cumulative bark beetle-caused tree mortality (1997–2012; gray, lower, middle [most realistic], and upper estimates) and forest fire-caused tree mortality (1984–2012; white, high and moderate+high severity) by state for (top) area (ha) and (bottom) percentage of forest area within each state.

and 1.1% of the total area of bark beetle-caused mortality area. When a higher threshold of 75% is applied (which is more conservative with respect to ensuring overlap within a grid cell), these numbers decrease to 28,144 ha or about 0.5% of fire-caused mortality. Three forest fires had relatively high amounts of prior beetle kill and may be worthy of additional study with finer resolution imagery and additional observations (such as weather): the Tripod Complex in northern Washington in 2007 (14,000 ha or 31% of fire-caused mortality had prior beetle kill using the 50% threshold); the High Park Fire in northern Colorado in 2012 (11,000 ha or 64%); and the Mustang Complex in central Idaho in 2012 (4,000 ha or 5%). These fires occurred within a few years of beetle activity, suggesting that killed trees potentially still had some red needles (Hicke et al. 2012b).

Discussion

Substantial tree mortality was caused by fires and bark beetle outbreaks in the western United States in recent decades. Using our most realistic (middle) estimate for bark beetles and the moderate+high severity estimate for fires, we calculated that more than 13% of the total forested area was killed (i.e., mortality area). This mortality area amount is 24–46% of the total affected area (areal estimates that include live trees), the metric often used in discussions on bark beetle or wildfire impacts. Although significant mortality occurred in the 1980s and 1990s, most of the mortality has occurred since 2000. Our most realistic estimate of mortality area from bark beetles exceeded that of the upper estimate from fires. Bark beetles killed trees over a greater spatial extent than forest fires, but typically caused lower mortality on a per grid cell basis. Outbreaks moved through a stand (grid cell) over the course of several years, in contrast to forest fires that occurred only in 1 year within a grid cell.

The influence of (mean) climate and forest type on disturbance type was apparent. Forest types consisting of ponderosa pine, Cali-

fornia mixed conifer, and nonforest in California experienced more tree-killing forest fires than bark beetle outbreaks. These forest types are associated with lower elevations, coastal California forests, and/or drier forests. In contrast, lodgepole pine, Douglas-fir, and spruce/fir forest types experienced more bark beetle outbreaks. These forest types are at higher elevations and/or are wetter and cooler than those discussed above, which led to the decreased amount of wildfire. However, we also note that these forest types experience longer fire return intervals (Romme 1982, Kulakowski et al. 2003) than our relatively short study period, and this factor also contributed to the reduced amount of mortality from wildfires. The wettest forests, on the coasts of northern California, Oregon, and Washington had very few fires or beetle outbreaks. Although no data are available on beetle outbreaks, our findings in these locations agree with studies of fire regime and fire return interval (Brown and Smith 2000, Rollins 2009).

Tree mortality in the western United States caused by bark beetles and fire is comparable to mortality from other processes and in other locations. Together the annual beetle- and fire-caused mortality areas are similar in magnitude to that from harvest in the same region, although harvesting from the reported period (2001–2005) has declined substantially from earlier periods (Smith et al. 2009).

The middle estimate of cumulative mortality from beetles in the western United States is close to that caused by the major outbreaks in British Columbia that have occurred since 2000 (Meddens et al. 2012). Kurz and Apps (1999) reported that the forests of western Canada experienced fire-caused mortality areas of 0.32 Mha/year during 1980–1989, which is somewhat higher than our estimate for the western United States. As with our estimates in the western United States, Canadian estimates of fire- and beetle-caused mortality are subject to uncertainty.

Whether the large extent of tree mortality in recent decades is unusual or unprecedented is not well understood. Littell et al. (2009) report that the amount of burned area occurring in the early

1900s is similar to that in recent decades, and it is likely that much of this early burned area was in forests, although the amount of tree-killing fire was not considered. A recent study of California fires found increasing amounts of high-severity fire during the last three decades (Miller et al. 2009); patterns in prior decades were not analyzed. Higher severity fires in recent decades than in past centuries have been reported for some locations (O'Connor et al. 2014). Major bark beetle outbreaks also occurred in the early 1900s (e.g., Cahill 1977), although their extent is also difficult to ascertain.

What was the influence of climate change on these disturbances? Although our study did not address influences, we briefly discuss what other studies have reported about this issue. The western United States was in severe drought for several years during the early 2000s,² which has been referred to as a “global-change-type drought” because of higher temperatures than in earlier droughts as a result of climate change (Breshears et al. 2005). During this period, the western United States experienced severe fires in Douglas-fir, ponderosa, lodgepole pine, and piñon-juniper forest types. In addition, multiple bark beetle species killed trees across the region during this time. Longer-term warming has led to earlier springs, longer fire seasons, and decreased fuel moistures (Westerling et al. 2006, Littell et al. 2009) and facilitated beetle outbreaks through increased winter survival, faster life stage development rates leading to shorter life cycle times and synchrony of attacking beetle populations, and greater host tree stress (e.g., Bentz et al. 2010, Creeden et al. 2014). These mechanistic links between the two forest disturbances and warmer, drier conditions have been well established (Pyne et al. 1996, Westerling et al. 2003, Raffa et al. 2008, Littell et al. 2009, Williams et al. 2013, Anderegg et al. 2015), and recent warming observed in the western United States has been attributed to anthropogenic climate change (Barnett et al. 2008, Abatzoglou et al. 2014). Thus, it is likely that recent anthropogenic warming influenced the large area of forest mortality, although more studies are needed to clarify this issue.

Other factors also played roles, in particular, forest policy and management. Fire management policies altered historical fire regimes during the 20th century, promoting fuel buildups and structure changes in many western forest types (Stephens et al. 2014). Fire policy has changed several times in the last two decades to begin reversing the effects of a century of suppression. Changes include extensive forest thinning, reintroduction of fire through prescription, and reduced suppression of wildfires in remote areas to restore ecological processes (Stephens and Ruth 2005, Stephens et al. 2012). After harvesting in the late 1800s and early 1900s, extensive forests established and by our study period were in age, size, and density conditions preferred by bark beetles (Shore and Safranyik 1992, Hicke and Jenkins 2008, Krist et al. 2014).

Our results are the first to quantify the area of tree mortality from wildfires and bark beetles over a large region using observational data sets. However, our estimates are subject to some uncertainty. To account for this uncertainty, we provide a range of estimates for both forest fires and bark beetles as described in the Methods. For bark beetle outbreaks, because our middle and upper estimates are based on comparisons with fine-resolution remotely sensed imagery that was classified with high accuracy, we feel that these are more realistic than the lower estimate. We suggest that the middle estimate is most realistic because additional comparisons with imagery resulted in lower values and because the middle estimate is more conservative. Regarding fire-caused tree mortality, we do not have information to suggest that one of the moderate+high- or high-se-

verity estimates is more likely to be accurate. Based on our expert opinion, we have medium confidence in the most realistic estimates (bark beetles: middle estimate; wildfires: range of estimates), and to improve estimates and confidence, additional studies are needed. Satellite remote sensing has been shown to accurately map bark beetle-caused tree mortality (e.g., Meddens et al. 2013), suggesting opportunities for improved estimates over large areas such as the western United States. Forest fires were mapped by analysts using consistently interpretable Landsat satellite data, implying more confidence in these estimates than in those from beetle outbreaks, which were generated by diverse aerial surveyors in airplanes. However, the spectral index (i.e., dNBR) and classification thresholds used were not designed specifically to measure tree mortality (Key and Benson 2006) and have been related to tree mortality in only two studies (Miller et al. 2009, Cansler and McKenzie 2012). Thus, development of indices and relationships to field quantification of mortality could reduce uncertainty in these estimates and improve automated mapping of fire-induced tree mortality. Furthermore, in high-elevation forests, even low-severity fires may kill trees (O'Connor et al. 2014). Finally, because we assume that 30-m pixels were 100% forest and 100% burned, the actual fire-caused mortality area is likely to be lower than our moderate+high (upper) estimate.

Conclusions

Our methods of estimating tree mortality area from fires and beetle outbreaks allowed us to compare the impact of each of these disturbance types as well as assess their magnitude relative to that of harvesting. The importance of considering mortality area instead of “affected area” or burn perimeter area was illustrated by the substantially smaller mortality area we found for these disturbances (between one-quarter and one-half of affected area or burn perimeter area). We suggest that mortality area is a better representation of the ecological impact of tree mortality caused by fires and beetles.

A significant fraction of forests in the western United States has been killed by fire and beetles in the last several decades. We find a range of mortality area resulting from uncertainties in the beetle- and fire-caused mortality estimates. Using our most realistic (middle) estimate for beetle outbreaks and upper estimate for wildfires, we found that bark beetles have killed more trees than fires in recent decades, and, together, these agents have killed a similar amount of trees in the western United States as has harvesting. Our spatially explicit analysis allowed us to characterize patterns of tree mortality. We found that, in general, fires were a more typical disturbance agent in lower elevation and coastal forests, whereas bark beetles were the main disturbance agent in higher elevation forests. However, we note that our study period was short relative to the typical fire return interval of higher elevation forests.

We should expect that forest fires and bark beetle outbreaks will continue to be important forest disturbances in the western United States, particularly given the magnitude of future warming anticipated in this region (Melillo et al. 2014) (although beetle-affected stands will take decades to become susceptible again to outbreaks). Therefore, establishing baselines of tree mortality after these disturbances is critical to detecting changes in forest patterns and processes and providing input for management responses and additional research. Our study provides an initial overview of these disturbances in recent years. Additional regional-scale studies of tree mortality from bark beetles and fire are needed to reduce current uncertainties and assess anticipated changes in these important forest disturbance processes.

Endnotes

1. For more information, see mtbs.gov.
2. For more information, see droughtmonitor.unl.edu

Literature Cited

- ABATZOGLOU, J.T., D.E. RUPP, AND P.W. MOTE. 2014. Seasonal climate variability and change in the Pacific Northwest of the United States. *J. Clim.* 27(5):2125–2142.
- ALLEN, C.D., D.D. BRESHEARS, AND N.G. MCDOWELL. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:art129.
- ALLEN, C.D., A.K. MACALADY, H. CHENCHOUNI, D. BACHELET, N. MCDOWELL, M. VENNETIER, T. KITZBERGER, ET AL. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259(4):660–684.
- ANDEREGG, W.R.L., J.A. HICKE, R.A. FISHER, C.D. ALLEN, J. AUKEMA, B. BENTZ, S. HOOD, ET AL. 2015. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist* 208(3):674–683.
- ANDEREGG, W.R.L., J.M. KANE, AND L.D.L. ANDEREGG. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* 3(1):30–36.
- BARNETT, T.P., D.W. PIERCE, H.G. HIDALGO, C. BONFILS, B.D. SANTER, T. DAS, G. BALA, ET AL. 2008. Human-induced changes in the hydrology of the western United States. *Science* 319:1080–1083.
- BENTZ, B.J., J. RÉGNIÈRE, C.J. FETTIG, E.M. HANSEN, J.L. HAYES, J.A. HICKE, R.G. KELSEY, J.F. NEGRÓN, AND S.J. SEYBOLD. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience* 60(8):602–613.
- BRESHEARS, D.D., N.S. COBB, P.M. RICH, K.P. PRICE, C.D. ALLEN, R.G. BALICE, W.H. ROMME, ET AL. 2005. Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci. USA* 102(42):15144–15148.
- BROWN, J.K., AND J.K. SMITH. 2000. *Wildland fire in ecosystems: Effects of fire on flora*. USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-42-vol. 2, Rocky Mountain Research Station, Ogden, UT. 257 p.
- CAHILL, D.B. 1977. *Net impact of spruce beetle outbreak on White River National Forest, 1939-1951*. USDA For. Serv., Rocky Mountain Regional Rep., Rocky Mountain Research Station, Fort Collins, CO. 46 p.
- CANSLER, C.A., AND D. MCKENZIE. 2012. How robust are burn severity indices when applied in a new region? Evaluation of alternate field-based and remote-sensing methods. *Remote Sens.* 4:456–483.
- CLIFFORD, M.J., M.E. ROCCA, R. DELPH, P.L. FORD, AND N.S. COBB. 2008. Drought induced tree mortality and ensuing bark beetle outbreaks in southwestern pinyon-juniper woodlands. P. 39–51 in *Ecology, management, and restoration of piñon-juniper and ponderosa pine ecosystems: Combined proceedings of the 2005 St. George, Utah and 2006 Albuquerque, New Mexico workshops*, Gottfried, G.J., J.D. Shaw, and P.L. Ford (eds.). USDA For. Serv., Proc. RMRS-P-51, Rocky Mountain Research Station, Fort Collins, CO.
- COLE, W.E., AND G.D. AMMAN. 1980. *Mountain pine beetle dynamics in lodgepole pine forests, part I: Course of an infestation*. USDA For. Serv., Gen. Tech. Rep. INT-89, Intermountain Forest and Range Experiment Station, Ogden, UT. 56 p.
- CREEDEN, E.P., J.A. HICKE, AND P.C. BUOTTE. 2014. Climate, weather, and recent mountain pine beetle outbreaks in the western United States. *For. Ecol. Manage.* 312:239–251.
- DALE, V.H., L.A. JOYCE, S. McNULTY, R.P. NEILSON, M.P. AYRES, M.D. FLANNIGAN, P.J. HANSON, ET AL. 2001. Climate change and forest disturbances. *BioScience* 51(9):723–734.
- EARLES, J.M., M.P. NORTH, AND M.D. HURTEAU. 2014. Wildfire and drought dynamics destabilize carbon stores of fire-suppressed forests. *Ecol. Applic.* 4:732–740.
- EIDENSHINK, J., B. SCHWIND, K. BREWER, Z. ZHU, B. QUAYLE, AND S. HOWARD. 2007. A project for monitoring trends in burn severity. *Fire Ecol.* 3(1):3–12.
- GERGELY, K.J., AND A. MCKERROW. 2013. *PAD-US: National inventory of protected areas*. US Geological Survey, Fact Sheet 2013–3086, Washington, DC. 1 p.
- GHIMIRE, B., C.A. WILLIAMS, G.J. COLLATZ, AND M. VANDERHOOF. 2012. Fire-induced carbon emissions and regrowth uptake in western US forests: Documenting variation across forest types, fire severity, and climate regions. *J. Geophys. Res.* 117(G3).
- HARPOLD, A.A., J.A. BIEDERMAN, K. CONDON, M. MERINO, Y. KORGANONKAR, T. NAN, L.L. SLOAT, M. ROSS, AND P.D. BROOKS. 2013. Changes in snow accumulation and ablation following the Las Conchas Forest Fire, New Mexico, USA. *Ecohydrology* 7:440–452.
- HICKE, J.A., C.D. ALLEN, A.R. DESAI, M.C. DIETZE, R.J. HALL, E.H.T. HOGG, D.M. KASHIAN, ET AL. 2012a. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biol.* 18(1):7–34.
- HICKE, J.A., AND J.C. JENKINS. 2008. Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. *For. Ecol. Manage.* 225:1536–1547.
- HICKE, J.A., M.C. JOHNSON, J.L. HAYES, AND H.K. PREISLER. 2012b. Effects of bark beetle-caused tree mortality on wildfire. *For. Ecol. Manage.* 271:81–90.
- HICKE, J.A., J.A. LOGAN, J. POWELL, AND D.S. OJIMA. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *J. Geophys. Res. Biogeosci.* 111:G02019.
- HICKE, J.A., A.J.H. MEDDENS, C.D. ALLEN, AND C.A. KOLDEN. 2013. Carbon stocks of trees killed by bark beetles and wildfire in the western United States. *Environ. Res. Lett.* 8(3):035032.
- HOMER, C., C. HUANG, L. YANG, B. WYLIE, AND M. COAN. 2004. Development of a 2001 national land cover database for the United States. *Photogramm. Eng. Remote Sens.* 70:829–840.
- HUTTO, R.L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (USA) conifer forests. *Conserv. Biol.* 9(5):1041–1058.
- KEY, C.H., AND N.C. BENSON. 2006. *Landscape assessment, ground measure of severity of the composition burn index and remote sensing severity. FIREMON: Fire effects of inventory system*. USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-164, Rocky Mountain Research Station, Fort Collins, CO. 55 p.
- KOLDEN, C.A., J.A. LUTZ, C.H. KEY, J.T. KANE, AND J.W. VAN WAGTEN-DONK. 2012. Mapped versus actual burned area within wildfire perimeters: Characterizing the unburned. *For. Ecol. Manage.* 286:38–47.
- KOLDEN, C.A., A.M.S. SMITH, AND J.T. ABATZOGLOU. 2015. Limitations and utilization of monitoring trends in burn severity products for assessing wildfire severity in the USA. *Int. J. Wildl. Fire* 24(7):1023–1028.
- KRIST, F.J., J.R. ELLENWOOD, M.E. WOODS, A.J. MCMAHAN, J.P. COWARDIN, D.E. RYERSON, F.J. SAPIO, M.O. ZWEIFLER, AND S.A. ROMERO. 2014. *2013–2027 National insect and disease forest risk assessment*. USDA For. Serv., FHTET-14-01, Forest Health Technology and Enterprise Team, Fort Collins, CO. 199 p.
- KULAKOWSKI, D., T.T. VEBLEN, AND P. BEBI. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *J. Biogeogr.* 30:1445–1456.
- KURZ, W.A., AND M.J. APPS. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol. Applic.* 9(2):526–547.
- LARSON, A.J., AND D. CHURCHILL. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *For. Ecol. Manage.* 267:74–92.
- LITTELL, J.S., D. MCKENZIE, D.L. PETERSON, AND A.L. WESTERLING. 2009. Climate and wildfire area burned in western US ecoprovinces, 1916–2003. *Ecol. Applic.* 19(4):1003–1021.

- LUTZ, J.A., A.J. LARSON, M.E. SWANSON, AND J.A. FREUND. 2012. Ecological importance of large-diameter trees in a temperate mixed-conifer forest. *PLoS One* 7(5):e36131.
- MARKHAM, B.L., J.C. STOREY, D.L. WILLIAMS, AND J.R. IRONS. 2004. Landsat sensor performance: History and current status. *IEEE Trans. Geosci. Remote Sens.* 42(12):2691-2694.
- MEDDENS, A.J.H., AND J.A. HICKE. 2014. Spatial and temporal patterns of Landsat-based detection of tree mortality caused by a mountain pine beetle outbreak in Colorado, USA. *For. Ecol. Manage.* 322:78-88.
- MEDDENS, A.J.H., J.A. HICKE, AND C.A. FERGUSON. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecol. Applic.* 22(7):1876-1891.
- MEDDENS, A.J.H., J.A. HICKE, L.A. VIERLING, AND A.T. HUDAK. 2013. Evaluating methods to detect bark beetle-caused tree mortality using single-date and multi-date Landsat imagery. *Remote Sens. Environ.* 132:49-58.
- MEIGS, G.W., R.E. KENNEDY, AND W.B. COHEN. 2011. A Landsat time series approach to characterize bark beetle and defoliator impacts on tree mortality and surface fuels in conifer forests. *Remote Sens. Environ.* 115(12):3707-3718.
- MELILLO, J.M., T.T.C. RICHMOND, AND G.W. YOHE (EDS.). 2014. *Climate change impacts in the United States: The Third National Climate Assessment*. US Global Change Research Program, Washington, DC. 841 p.
- MIKKELSON, K.M., E.R.V. DICKENSON, R.M. MAXWELL, J.E. MCCRAY, AND J.O. SHARP. 2013. Water-quality impacts from climate-induced forest die-off. *Nat. Clim. Change* 3(3):218-222.
- MILLER, J.D., E.E. KNAPP, C.H. KEY, C.N. SKINNER, C.J. ISBELL, R.M. CREAMY, AND J.W. SHERLOCK. 2009. Calibration and validation of the relative differenced normalized burn ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. *Remote Sens. Environ.* 113(3):645-656.
- NATIONAL RESEARCH COUNCIL. 2011. *Climate stabilization targets: Emissions, concentrations, and impacts over decades to millennia*. The National Academies Press, Washington, DC. 298 p.
- O'CONNOR, C.D., D.A. FALK, A.M. LYNCH, AND T.W. SWETNAM. 2014. Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleno Mountains, Arizona, USA. *For. Ecol. Manage.* 329:264-278.
- PUGH, E., AND E. GORDON. 2012. A conceptual model of water yield effects from beetle-induced tree death in snow-dominated lodgepole pine forests. *Hydrol. Processes* 27(14):2048-2060.
- PYNE, S.J., P.L. ANDREWS, AND R.D. LAVEN. 1996. *Introduction to wildland fire*. John Wiley & Sons, New York. 808 p.
- 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.
- ROBICHAUD, P.R. 2000. Fire effects on infiltration rates after prescribed fire in Northern Rocky Mountain forests, USA. *J. Hydrol.* 231-232:220-229.
- ROLLINS, M.G. 2009. LANDFIRE: A nationally consistent vegetation, wildland fire, and fuel assessment. *Int. J. Wildl. Fire* 18:235-249.
- ROMME, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecol. Monogr.* 52:199-221.
- RUEFENACHT, B., M.V. FINCO, M.D. NELSON, R. CZAPLEWSKI, E.H. HELMER, J.A. BLACKARD, G.R. HOLDEN, ET AL. 2008. Conterminous US and Alaska forest type mapping using Forest Inventory and Analysis data. *Photogramm. Eng. Remote Sens.* 74(11):1379-1389.
- SAAB, V.A., Q.S. LATIF, M.M. ROWLAND, T.N. JOHNSON, A.D. CHALFOUN, S.W. BUSKIRK, J.E. HEYWARD, AND M.A. DRESSER. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. *For. Sci.* 60(3):539-559.
- SHORE, T.L., AND L. SAFRANYIK. 1992. *Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands*. Inform. Rep. BC-X-336, Forestry Canada, Pacific Forestry Centre, Victoria, BC, Canada. 17 p.
- SMITH, W.B., P.D. MILES, C.H. PERRY, AND S.A. PUGH. 2009. *Forest resources of the United States, 2007*. USDA For. Serv., Gen. Tech. Rep. WO-78, Washington, DC. 336 p.
- STEPHENS, S.L., N. BURROWS, A. BUYANTUYEV, R.W. GRAY, R.E. KEANE, R. KUBIAN, S. LIU, ET AL. 2014. Temperate and boreal forest mega-fires: Characteristics and challenges. *Front. Ecol. Environ.* 12:115-122.
- STEPHENS, S.L., J.D. MCIVER, R.E.J. BOERNER, C.J. FETTIG, J.B. FONTAINE, B.R. HARTSOUGH, P.L. KENNEDY, AND D.W. SCHWILK. 2012. The effects of forest fuel-reduction treatments in the United States. *BioScience* 62(6):549-560.
- STEPHENS, S.L., AND L.W. RUTH. 2005. Federal forest-fire policy in the United States. *Ecol. Applic.* 15(2):532-542.
- SWANSON, M.E., J.F. FRANKLIN, R.L. BESCHTA, C.M. CRISAFULLI, D.A. DELLA SALA, R.L. HUTTO, D.B. LINDENMAYER, AND F.J. SWANSON. 2010. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Front. Ecol. Environ.* 9:117-125.
- TURNER, M.G., W.H. ROMME, AND D.B. TINKER. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Front. Ecol. Environ.* 1(7):351-358.
- USDA FOREST SERVICE. 2005. *Aerial survey geographic information system handbook*. Forest Health Monitoring Program. Available online at www.fs.fed.us/foresthealth/technology/pdfs/GISHandbook_body_apndx-A-C.pdf; last accessed Nov. 9, 2015.
- USDA FOREST SERVICE. 2004. *Forest insect and disease conditions in the United States, 2003*. USDA For. Serv., Washington, DC. 156 p.
- VAN MANTGEM, P.J., N.L. STEPHENSON, J.C. BYRNE, L.D. DANIELS, J.F. FRANKLIN, P.Z. FULE, M.E. HARMON, ET AL. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323(5913):521-524.
- VEBLEN, T.T., K.S. HADLEY, M.S. REID, AND A.J. REBERTUS. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72(1):213-231.
- WEED, A.S., M.P. AYRES, AND J.A. HICKE. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecol. Monogr.* 84:441-470.
- WESTERLING, A.L., T.J. BROWN, A. GERSHUNOV, D.R. CAYAN, AND M.D. DETTINGER. 2003. Climate and wildfire in the western United States. *Bull. Am. Meteorol. Soc.* 84(5):595-604.
- WESTERLING, A.L., H.G. HIDALGO, D.R. CAYAN, AND T.W. SWETNAM. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313(5789):940-943.
- WILLIAMS, A.P., C.D. ALLEN, A.K. MACALADY, D. GRIFFIN, C.A. WOODHOUSE, D.M. MEKO, T.W. SWETNAM, ET AL. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change* 3(3):292-297.
- WILLIAMS, D.W., AND R. BIRDSEY. 2003. *Historical patterns of spruce budworm defoliation and bark beetle outbreaks in North American conifer forests: An atlas and description of digital maps*. USDA For. Serv., Gen. Tech. Rep. GTR-NE-308, Northeastern Research Station, Newtown Square, PA. 33 p.
- WULDER, M.A., C.C. DYMOND, J.C. WHITE, D.G. LECKIE, AND A.L. CARROLL. 2006. Surveying mountain pine beetle damage of forests: A review of remote sensing opportunities. *For. Ecol. Manage.* 221(1-3):27-41.
- ZHU, Z., AND J. EIDENSHINK. 2007. Assessment of spatial and temporal trends of fire severity in the United States. In *Proceedings of the 4th International Wildland Fire Conference, 2007 May 14-17, Sevilla, Spain*. ISDR and FAO, Sevilla, Spain. 6 p.
- ZHU, Z., C.H. KEY, D. OHLEN, AND N.C. BENSON. 2006. *Evaluate sensitivities of burn-severity mapping algorithms for different ecosystems and fire histories in the United States*. Joint Fire Sci. Project 01-1-4-12, US Geological Science, National Center for Earth Resources Observation and Science, Sioux Falls, SD. 35 p.