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Does wildfire likelihood increase following insect outbreaks in conifer forests?

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Abstract. Although there is acute concern that insect-caused tree mortality increases the likelihood or severity of subsequent wildfire, previous studies have been mixed, with findings typically based on stand-scale simulations or individual events. This study investigates landscape- and regional-scale wildfire likelihood following outbreaks of the two most prevalent native insect pests in the US Pacific Northwest (PNW): mountain pine beetle (MPB; *Dendroctonus ponderosae*) and western spruce budworm (WSB; *Choristoneura freemani*). We leverage seamless census data across numerous insect and fire events to (1) summarize the interannual dynamics of insects (1970–2012) and wildfires (1984–2012) across forested ecoregions of the PNW; (2) identify potential linked disturbance interactions with an empirical wildfire likelihood index; (3) quantify this insect-fire likelihood across different insect agents, time lags, ecoregions, and fire sizes. All three disturbance agents have occurred primarily in the drier, interior conifer forests east of the Cascade Range. In general, WSB extent exceeds MPB extent, which in turn exceeds wildfire extent, and each disturbance typically affects less than 2% annually of a given ecoregion. In recent decades across the PNW, wildfire likelihood does not consistently increase or decrease following insect outbreaks. There is evidence, however, of linked interactions that vary across insect agent (MPB, WSB), space (ecoregion), and time (interval since insect onset). Specifically, in most cases following MPB activity, fire likelihood is neither higher nor lower than in non-MPB-affected forests. In contrast, fire likelihood is lower following WSB activity across multiple ecoregions and time lags. In addition, insect-fire likelihood is not consistently associated with interannual fire extent, suggesting that other factors (e.g., climate) control the disproportionately large fire years accounting for regional fire dynamics. Thus, although both bark beetles and defoliators alter fuels and associated fire potential, the windows of opportunity for increased or decreased fire likelihood are too narrow—or the phenomena themselves too rare—for a consistent signal to emerge across PNW conifer forests. These findings suggest that strategic plans should recognize (1) the relative rarity of insect-fire interactions and (2) the potential ecosystem restoration benefits of native insect outbreaks, when they do occur.

Key words: bark beetle; *Choristoneura freemani*; defoliator; *Dendroctonus ponderosae*; disturbance interactions; fire; forest health; mountain pine beetle; Pacific Northwest; western spruce budworm.

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INTRODUCTION

Insects and wildfires are important disturbance agents, shaping forest pattern and process throughout the world (e.g., Schelhaas et al. 2003, Kurz et al. 2008). In western North America, insect outbreaks and wildfires have influenced forests for millennia, both have been widespread in recent years, and both are projected to increase with anthropogenic climate change (e.g., Swetnam and Lynch 1993, McKenzie et al. 2004, Heyerdahl et al. 2008, Raffa et al. 2008, Littell et al. 2010). Recognizing that disturbances do not function in isolation, ecologists have focused increasingly on the often complex interactions among multiple disturbances (e.g., Paine et al. 1998, Simard et al. 2011). Indeed, acute societal concerns that insects alter fuels and amplify wildfire susceptibility have prompted numerous investigations of insect-fire interactions (Hicke et al. 2012, Jenkins et al. 2012). Results to date have been mixed, however, with evidence of positive (e.g., Perrakis et al. 2014, Prichard and Kennedy 2014), negative (e.g., Lynch and Moorcroft 2008, Simard et al. 2011, Cohn et al. 2014), and neutral (e.g., Crickmore 2011, Kulakowski and Jarvis 2011, Flower et al. 2014) effects of insects on subsequent fire likelihood, behavior, or severity.

Much of the incongruence in the literature is attributable to differences in the type and spatiotemporal scale of analysis, the conceptualization of disturbance interactions, and the timing and type of insect outbreak. Many recent studies of insect-fire interactions use simulation models to evaluate fire behavior and/or effects in insect-altered forests at the stand scale (e.g., Page and Jenkins 2007, Simard et al. 2011). Although integral for understanding mechanistic relationships among insects, fuels, and fire, this simulation approach assumes that an insect-affected stand actually burns. In reality, insects and wildfires affect only a small portion of forested landscapes in a given year, even in regional outbreak or fire years (Littell et al. 2009, Meigs et al. 2015). Other studies have assessed insect-fire interactions in actual wildfire events (e.g., Lynch et al. 2006, Kulakowski and Veblen 2007, Prichard and Kennedy 2014), but these empirical assessments typically have been limited to individual fires or insect outbreaks (Bisrat 2010). We suggest that a more systematic, regional approach is necessary to elucidate general system behavior across numerous insect and fire events. This study integrates spatially and temporally seamless insect and fire census data to assess insect-wildfire interactions across a 40 million hectare region, the US Pacific Northwest (Oregon and Washington; hereafter "PNW"; Fig. 1; Appendix A).

A second source of ambiguity in the literature is that studies have conceptualized disturbance interactions differently, recognizing their many potential manifestations (e.g., at different spatiotemporal scales, with or without causal relationships). Whereas the concept of "compound" disturbances (sensu Paine et al. 1998) emphasizes the synergistic impacts and unpredictable responses of disturbance events occurring in rapid succession, the concept of "linked" disturbances emphasizes the effects that one disturbance has on the likelihood, severity, or extent of a subsequent disturbance (Simard et al. 2011, Harvey et al. 2013). Here, we investigate one aspect of linked disturbance interactions, focusing on the likelihood of wildfire following insect outbreaks. Specifically, we test if fire likelihood is higher or lower following insect outbreaks than would be expected given the random occurrence of both disturbances. Importantly, any non-random co-occurrence has ecological significance whether the two disturbances are linked mechanistically or are responding to other drivers. Indeed, because the same abiotic and biotic drivers (e.g., drought, forest structure, and landscape contiguity) are associated with both insect outbreaks and wildfires (Simard et al. 2011, Flower et al. 2014, Prichard and Kennedy 2014), they may co-occur without a strong causal relationship. Nevertheless, to address concerns that forest managers and policy makers have about insect-fire interactions, it is essential to quantify the fundamental co-occurrence of insects and wildfires at landscape and regional scales.

A third key factor accounting for mixed results in the insect-fire interaction literature is that insect effects on fuels and fire behavior vary with insect timing and type (Hicke et al. 2012, Flower et al. 2014). This study assesses fire likelihood at multiple time lags following outbreaks of the two most prevalent native insect pests in the PNW: mountain pine beetle (MPB; *Dendroctonus ponder-*
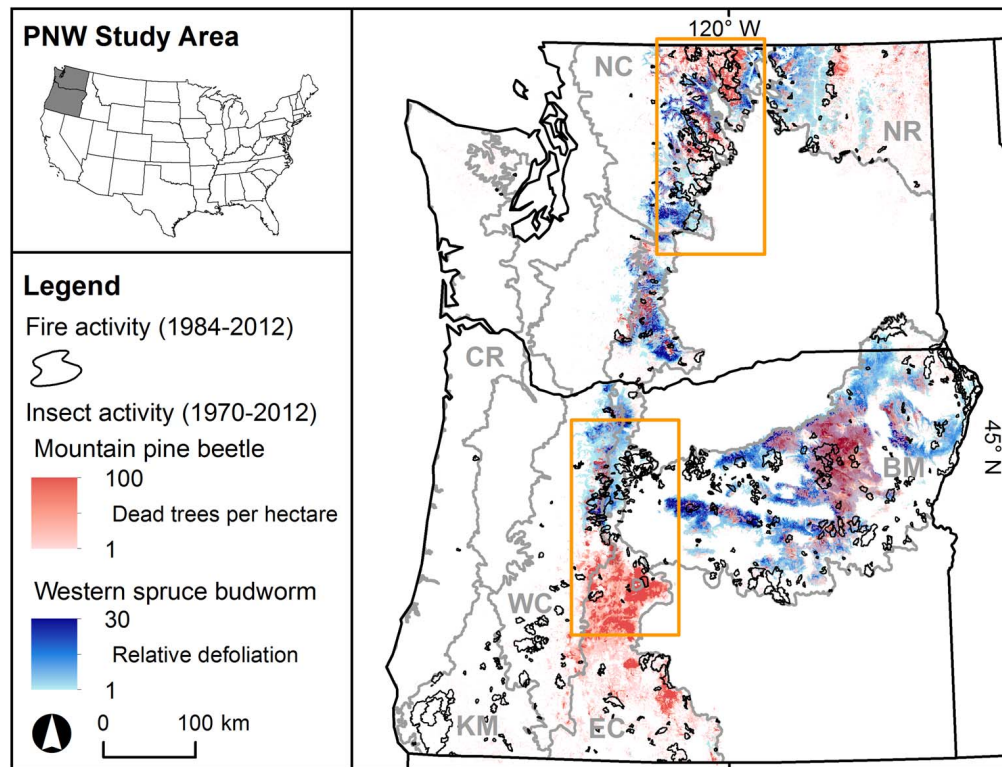
Fig. 1. Study area map and distribution of insects and wildfires across forested ecoregions of the Pacific Northwest (PNW; Oregon and Washington; inset). Fire perimeters are clipped within forested ecoregion and state boundaries ($n = 685$; http://mtbs.gov). Cumulative insect activity from aerial detection surveys (ADS; see *Methods*). Note that mountain pine beetle (MPB; red) and western spruce budworm (WSB; blue) have been active primarily in the dry, interior conifer forests east of the crest of the Cascade Range, whereas wildfire has been distributed widely in the interior forests as well as portions of the WC and KM ecoregions. All three disturbances have been absent in the CR. Note also that MPB overlaps WSB activity in this display (MPB shown with 30% transparency), revealing purple locations with both insects. OR and WA encompass ca. 40,000,000 ha, total forest extent in forested ecoregions is ca. 20,000,000 ha (Appendix B), and the total area affected by either insect is ca. 8,000,000 ha according to ADS data (1970–2012). Orange rectangles denote extent of zoom maps in Appendix C. Forested ecoregion (level three; Omernik 1987) abbreviations: NC: North Cascades; NR: Northern Rockies; CR: Coast Range; BM: Blue Mountains; WC: West Cascades; EC: East Cascades; KM: Klamath Mountains. We include only the portions of ecoregions within Oregon and Washington.

osae Hopkins [Coleoptera: Curculionidae: Scolytinae]; a bark beetle) and western spruce budworm (WSB; *Choristoneura freemani* Razowski [Lepidoptera: Tortricidae]; a defoliator) (Williams and Birdsey 2003, Meigs et al. 2015). Outbreaks of both insects are associated with endogenous (e.g., insect population dynamics, host tree vigor and distribution) and exogenous factors (e.g., short- and long-term climate variability; Sanders et al. 1985, Waring and Pitman 1985, Waring et al. 1992, Raffa et al. 2008, Bentz et al. 2010). During sustained outbreaks, both insects can cause pervasive tree mortality and associated changes in forest composition and fuel structure, although the mechanisms and rates differ (Swetnam and Lynch 1993, Raffa et al. 2008, Meigs et al. 2011). MPB adults mass attack the cambium of host trees (*Pinus* spp., especially mature lodgepole pine [*P. contorta* Douglas ex Louden]; Furniss and Carolin 1977, Raffa et al. 2008), causing variable but relatively rapid tree mortality across large areas (e.g., recent regional-scale outbreaks in British Columbia, US Rocky Mountains, and US PNW [Meddens et al. 2012, Preisler

et al. 2012, Meigs et al. 2015]). In contrast, WSB larvae typically consume the current year's foliage of host trees (primarily understory true fir [*Abies* spp.], spruce [*Picea* spp.], and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco]; Furniss and Carolin 1977, Sanders et al. 1985), resulting in relatively more gradual impacts on tree mortality and associated fuel dynamics (Hummel and Agee 2003, Meigs et al. 2011).

Although MPB effects on fuels and fire potential have been studied intensively, empirical evidence of linked disturbance interactions has been weak or lacking (e.g., Negron et al. 2008, Kulakowski and Jarvis 2011, Simard et al. 2011, Hicke et al. 2012, Harvey et al. 2013, but see Perrakis et al. 2014, Prichard and Kennedy 2014). Fewer studies to date have analyzed WSB-fire interactions, demonstrating negative feedbacks in British Columbia (Lynch and Moorcroft 2008), limited WSB effects on simulated fire behavior in Washington (Hummel and Agee 2003), no detectable WSB effects on burn severity in Oregon (Crickmore 2011), and a lack of WSB-fire synergism in Oregon, Idaho, and Montana (Flower et al. 2014). For both insects, time since outbreak is a particularly important factor for fuel succession and fire potential, as dead trees transition through characteristic stages with highly variable effects on surface, ladder, and crown fuels and associated fire behavior or effects (e.g., Hicke et al. 2012, Donato et al. 2013).

In recent decades across western North America, both MPB and WSB have erupted in extensive outbreaks (Williams and Birdsey 2003, Raffa et al. 2008), and wildfire extent has increased in association with longer, hotter fire seasons (Westerling et al. 2006, Littell et al. 2009). If insect outbreaks further increase wildfire likelihood, then these disturbance interactions have profound implications for forest management and policy. In the PNW, regional census data capture the spatiotemporal patterns of insect and wildfire activity over recent decades, providing a unique opportunity to assess the potential for linked disturbance interactions in a retrospective, empirical framework. Working at landscape and regional scales across numerous insect and fire events, our research objectives are to: (1) summarize the interannual dynamics of mountain pine beetle, western spruce budworm, and wildfire across forested ecoregions of the PNW; (2) identify potential linked disturbance interactions where wildfire likelihood is higher or lower than expected given the random occurrence of both disturbances; (3) quantify this insect-fire likelihood across different insect agents, time lags, ecoregions, and fire sizes from 1984 to 2012. We hypothesize that: (1) all three disturbances occur primarily in conifer forests east of the crest of the Cascade Range due to favorable climate, vegetation composition and structure, and ignition; (2) insects and wildfires exhibit linked disturbance interactions due to the relatively strong influence of insect-altered fuels versus other fire drivers; (3) wildfire likelihood varies with insect agent and time since outbreak due to differences in the timing and cumulative impacts of insects on tree mortality, fuel profiles, and altered fire potential. Through these three inter-related objectives and hypotheses, we address the overarching question: Does wildfire likelihood increase following insect outbreaks in conifer forests?

METHODS

Study area and design

The US Pacific Northwest is a geographically diverse region with ecologically, economically, and socially important forest landscapes. Conifer forests here are widespread, and their composition, structure, and productivity vary across gradients of climate, topography, soil parent material, disturbance regime, and management history (Franklin and Dyrness 1973, Hessburg et al. 2000, Meigs 2014). Although precipitation and temperature regimes are variable across the region, a common climatic feature is that little precipitation occurs in summer months (Franklin and Dyrness 1973). These relatively warm, dry conditions, coupled with abundant biomass and slow decomposition, are conducive to periodic insect and wildfire disturbances (e.g., Littell et al. 2010). In general, these forests occur in remote, mountainous terrain and are managed primarily by federal agencies for multiple resource objectives.

This observational study is retrospective, leveraging spatially and temporally extensive datasets encompassing all forested lands of the PNW. We define our scope of inference as the generally forested ecoregions (Omernik 1987),

which contain ca. 20 million hectares of forest, and the years covered by the census data (1970–2012 for insect data; 1984–2012 for fire data; Fig. 1; Appendix B). For the wildfire likelihood analysis (below), our scope is limited to forested pixels and to those years in which fire occurred in a given ecoregion. Recognizing that each ecoregion encompasses a range of forest conditions (e.g., potential vegetation type, composition, structure, and disturbance/management history), we conduct geospatial analyses at a relatively fine spatial grain (30 m) before interpreting results at broader ecoregional and regional scales. Given the widespread extent of similar geographic conditions, vegetation types, and anthropogenic pressures, the recent insect and wildfire dynamics in PNW forests are broadly representative of contemporary disturbance regimes in conifer forests of western North America.

Insect data from aerial detection surveys (ADS)

We accounted for MPB and WSB activity with geospatial data from the ADS, a cooperative effort between federal and state agencies conducted nationally and administered at the regional scale. These surveys have been flown since 1947 in US Forest Service Region 6 (Oregon and Washington; data available online: http://www.fs.usda.gov/main/r6/forest-grasslandhealth/), with observers in fixed-wing aircraft recording a wide range of forest insects and diseases based on aerial signatures in specific host trees and forest types (Ciesla 2006). Although ADS data provide an unmatched record of forest disturbances, there are important limitations related to the spatial and temporal variability of observation conditions, methodology, and personnel (Meigs et al. 2011, Meddens et al. 2012, Preisler et al. 2012). Due to these uncertainties, ADS data are intended for assessment of landscape-to-regional dynamics rather than specific points on the ground (Ciesla 2006, Meigs et al. 2011). To this end, we interpret insect patterns at ecoregional and regional scales and integrate multiple years of ADS data to estimate cumulative prefire insect activity.

We utilized ADS data on MPB and WSB from 1970 to 2012 (Fig. 1), converting the polygons to raster format (30-m grain) for further analysis. For each affected pixel, we identified the onset

(first year of detection), cumulative magnitude (dead trees ha^{-1} for MPB, defoliation units on a 1–3 scale for WSB), cumulative extent (ha), and count of years detected after Meigs et al. (2015).

Fire data from Monitoring Trends in Burn Severity (MTBS)

We assessed annual fire extent data from MTBS, a national effort to track fire extent and severity consistently (Eidenshink et al. 2007; http://mtbs.gov/). In the western US, the MTBS program maps all fires greater than 404 ha since 1984 using before-after change detection with Landsat TM/ETM+ imagery (30-m grain; Eidenshink et al. 2007). MTBS analysts use the normalized burn ratio spectral index (Key and Benson 2006) to delineate fire perimeters and compute severity.

We clipped fire perimeters within forested ecoregions (Omernik 1987) and state boundaries ($n = 685$ fire polygons; Fig. 1). As with the ADS data, we converted the polygons to raster format for spatial analysis at 30-m resolution. For this assessment, we included all area within fire perimeters. We recognize that there is substantial variability in burn severity, including unburned areas, within MTBS perimeters (Kolden et al. 2012), but our goal was to assess all potential overlap with the similarly inclusive and coarse-resolution insect polygon data.

Data summary and computations

To address our first objective, we mapped the three disturbance agents (MPB, WSB, and wildfire) and summarized interannual dynamics across the PNW. We included the full MTBS record (1984–2012) and additional years of ADS data (1970–2012) to capture a more extensive range of prefire insect activity for the earlier fire years (minimum 14 years for 1984 fires; maximum 42 years for 2012 fires).

For our second objective, we derived an empirical wildfire likelihood index in areas with and without prior insect activity. To this end, we integrated the ADS and MTBS data in a binary, two-by-two likelihood matrix of fire and insect activity (Appendix D). For each fire year (1984–2012), we computed fire extent with prior insect extent (A), unburned extent with prior insect extent (B), fire extent without prior insect extent (C), and the total remaining forest extent in each ecoregion

with neither fire nor prior insect extent (D). Then, for all pixels in a given year and ecoregion, we calculated empirical wildfire likelihood as the percent burned of the available area that did and did not have prior insects (Appendix D):

1. Fire likelihood in areas with prior insect activity: FL_I: $A/(A + B) \times 100$;
2. Fire likelihood in areas without prior insect activity: FL_{NI}: $C/(C + D) \times 100$.

Finally, by comparing these indices, we determined if fire likelihood is higher ($FL_I > FL_{NI}$) or lower ($FL_I < FL_{NI}$) in insect-affected areas than expected given the random occurrence of both disturbances ($FL_I = FL_{NI}$; see *Methods: Statistical and uncertainty analysis*).

To address our third objective, we compared fire likelihood with and without prior insect activity for each insect agent and ecoregion across multiple time lags, recognizing the importance of time since outbreak in fuel succession and fire potential (Hicke et al. 2012). For our overall summary and most inclusive calculation, we retained any prefire insect activity for a given fire year (range: 14–42 years). We also assessed fire likelihood in areas with and without onset of MPB or WSB outbreak in five year intervals (1–5, 6–10, 11–15, and 16–20). To retain as much of the fire population as possible in the full analysis of time since outbreak, we included intervals up to 20 years only (i.e., our ADS data begin in 1970, so all fires from 1990 onward have the potential for all insect time lags up to 20 years).

Finally, we assessed the effect of fire size on insect-fire likelihood by relating the difference in fire likelihood between areas with and without prior insect activity to the total fire extent in a given year. The years in our sample population vary considerably in interannual fire extent (Fig. 2), and this analysis enabled us to examine whether insect-affected areas were more or less likely to burn in years with few/small fires versus many/large fires (i.e., regionally synchronous, climate-driven fire years; Heyerdahl et al. 2008).

Statistical and uncertainty analysis

We conducted all geospatial analyses on rasterized insect and fire data at a 30-m grain with the ARCGIS, IDL, or GDAL programs, and we derived statistics and graphics with R (plyr,

ggplot2 packages; Wickham 2009, Wickham 2011). To mitigate the confounding effect of fire in nonforested areas, we limited the fire likelihood analysis to forested areas with an existing forest mask (30-m grain; Ohmann et al. 2012), based on USGS GAP and NLCD maps (data available online: http://gapanalysis.nbii.gov/, http://landcover.usgs.gov/; see Appendix A for acronym glossary and Appendix B for forest extent by ecoregion).

For each likelihood comparison, the core analysis was a paired difference between the percent burned of the available area with and without prior insect activity at the scale of individual fire years. After determining that these differences were not temporally autocorrelated but did exhibit outliers and positive skewness, we used a nonparametric test (Wilcoxon signed-rank, abbreviated SR). Because we tested these differences separately for each ecoregion, insect agent, and time interval (60 simultaneous comparisons), we used the false discovery rate (FDR; Benjamin and Hochberg 1995, Pike 2011) to control for potential Type I errors. Concurrently, we interpreted FDR-adjusted $P < 0.05$ as strong evidence of differences and FDR-adjusted $P < 0.1$ as moderate evidence, reducing potential Type II errors after Donato et al. (2013). We note that because we focused on fire likelihood for all years in which fire occurred (i.e., we excluded years with no fire extent), actual annual fire likelihood rates are slightly lower than our estimates. In addition, our fire likelihood metrics are similar to a recent conditional probability analysis of bark beetle-fire interactions (Bisrat 2010), but we cover many more years, use much finer-grained data, and focus on a specific bark beetle and defoliator.

For the time lag analysis, we treated the first year of ADS detection as the onset of insect outbreak, recognizing that actual insect activity likely initiated one year before it was observed by aerial surveyors (Kulakowski and Veblen 2007, Meddens et al. 2012). We also considered alternative metrics for timing of insect outbreak, such as peak year or last year of outbreak, but the onset year was a more consistent metric across such a wide range of fire and insect events. We address some of the uncertainty in the timing of insect onset and peak damage by focusing on five year intervals rather than individual years.
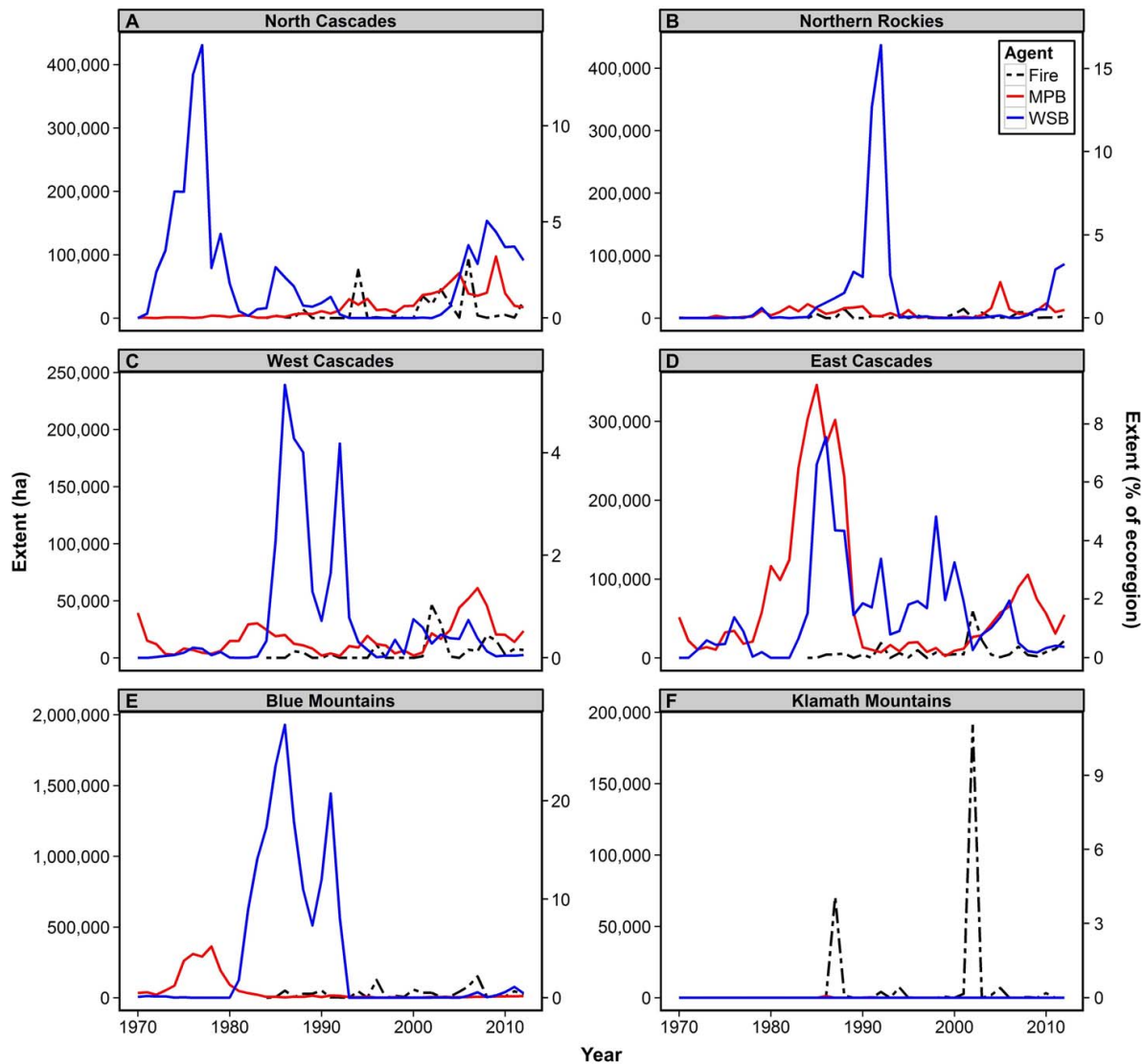
Fig. 2. Wildfire (black), mountain pine beetle (MPB; red), and western spruce budworm (WSB; blue) activity across forested ecoregions of the PNW. Note that insect extent, particularly WSB, is much greater than interannual and cumulative fire extent (except for Klamath Mountains). Note also the relatively continuous insect occurrence and more sporadic fire occurrence. Coast Range ecoregion excluded due to negligible insect and fire activity. Fire extent from perimeters (MTBS; 1984–2012; http://mtbs.gov) within forested ecoregion and state boundaries. Insect activity from aerial detection surveys (ADS; 1970–2012; see *Methods*).

RESULTS

Interannual dynamics of bark beetles, defoliators, and wildfires across the PNW

The three disturbances we assessed—MPB, WSB, and wildfire—have not been distributed evenly across space and time (Figs. 1 and 2). MPB and WSB have been active primarily in the drier, interior PNW forests east of the crest of the Cascade Range, whereas wildfire has occurred throughout interior forests as well as portions of the West Cascades and Klamath Mountains. In all ecoregions except for the Klamath Mountains, cumulative WSB extent has exceeded cumulative MPB extent, which in turn has exceeded wildfire extent (Fig. 2). In most years, the extent of any of

the three disturbances has been less than 2% of the available ecoregion area (Fig. 2). In general, insect outbreaks have occurred continuously over the course of several years, whereas wildfires have occurred more sporadically (Fig. 2).

Each ecoregion has illustrated a distinct disturbance history since 1970. The eastern North Cascades experienced all three disturbances in abundance (Fig. 1; Appendix C), particularly after 2000 (Fig. 2A). The Northern Rockies had widespread WSB activity, particularly in the 1990s (ca. 15% of the ecoregion [400,000 ha]), moderate MPB, and minimal fire (Fig. 2B). The West Cascades experienced a substantial WSB outbreak in the 1980s and 1990s and all three disturbances later in the time series (Fig. 2C), while the East Cascades had widespread outbreaks of both insects and relatively low fire extent (Fig. 2D). The Blue Mountains experienced the most widespread natural disturbance, dominated by WSB outbreaks in the 1980s encompassing more than 25% of the ecoregion (ca. 2,000,000 ha; Fig. 2E). The Klamath Mountains had major fire episodes—punctuated by the ca. 200,000 ha Biscuit Fire in 2002 (ca. 10% of the ecoregion)—but minimal insect activity (Fig. 2F). We thus exclude the Klamath Mountains from the insect-fire results and discussion below. Similarly, because the Coast Range was virtually devoid of fire and both insect species (logging has been the dominant recent disturbance; Spies et al. 2007), we exclude that ecoregion from further results and discussion.

Wildfire likelihood with and without recent insect activity

In recent decades across the PNW, wildfire likelihood has not been consistently associated with prefire insect outbreaks (Fig. 3). Fire likelihood was generally low (average median percent burned of available forest: 0.12%; Fig. 3; Appendix E: Table E1), and the relationship of fire likelihood and prefire insect outbreaks varied by agent and ecoregion. Specifically, when accounting for all possible years of prefire insect activity (range: 14–42 years), fire likelihood was higher following MPB activity in the North Cascades and West Cascades (FDR-adjusted $P < 0.05$; SR test), as well as across the combined forested ecoregions (FDR-adjusted $P < 0.1$; SR test; Fig. 3). In contrast, fire likelihood was lower following WSB activity in the Northern Rockies and Blue Mountains (FDR-adjusted $P < 0.1$; SR test; Fig. 3). Across all other combinations of insect agent and ecoregion, however, there were no apparent differences in fire likelihood between areas with and without prior insect activity, although fire likelihood following insect activity tended to be more variable (Fig. 3; Appendix E: Table E1).

Insect-fire likelihood across different insect agents, time lags, ecoregions, and fire sizes

MPB and WSB associations with fire likelihood were more evident in different time intervals since insect onset, signaling important time lags, but these associations were inconsistent among insects and ecoregions (Figs. 4 and 5; Appendix E). For example, fire likelihood was higher in MPB-affected forests than in non-MPB-affected forests within five years of outbreak onset in the North Cascades and across all forested ecoregions, whereas fire likelihood was lower following MPB outbreaks at particular time lags in the Northern Rockies, East Cascades, and Blue Mountains (FDR-adjusted $P < 0.1$; SR test; Fig. 4; Appendix E: Table E2). In most cases, however, fire likelihood was neither higher nor lower following MPB activity (Fig. 4; Appendix E: Table E2). In contrast, fire likelihood was consistently lower following WSB activity at multiple time lags in all ecoregions (FDR-adjusted $P < 0.1$; SR test; Fig. 5; Appendix E: Table E3).

There were no clear associations between fire likelihood and fire size (annual fire extent) for either insect at the ecoregional or regional scales (Fig. 6). Most years had relatively low total fire extent and small differences between forests with and without prior insect activity, although variability in the insect-fire signal increased with fire extent. One particularly extreme fire year in the North Cascades (driven by the 2006 Tripod Fire [ca. 70,000 ha]) illustrated very high fire extent and increased likelihood of fire in forests with a recent/ongoing MPB outbreak (Fig. 6A; Appendix C; Prichard and Kennedy 2014). Similarly, in the West Cascades, the 2003 B&B Fire (ca. 37,000 ha) occurred in an area with widespread, substantial WSB activity 10–15 years earlier (Fig. 6C; Appendix C; Crickmore
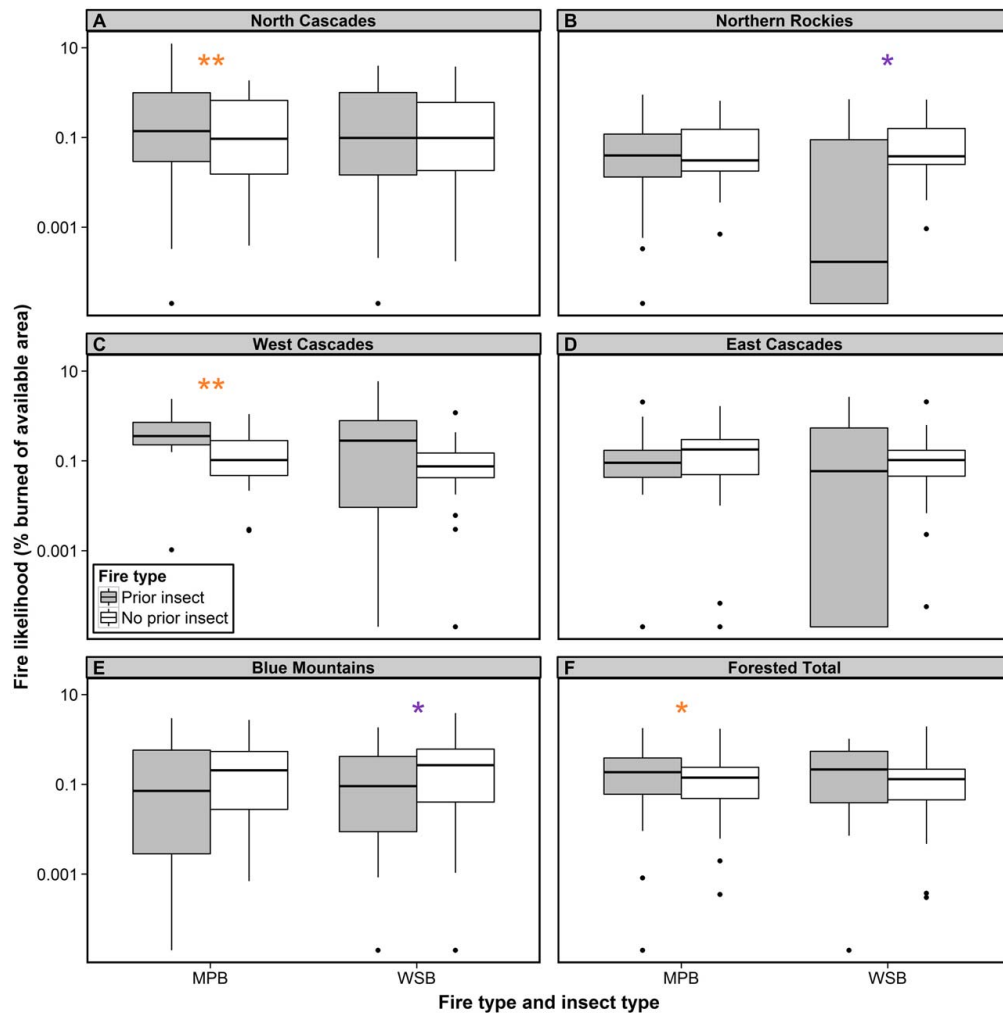
Fig. 3. Interannual fire likelihood with and without recent insect activity across forested ecoregions of the PNW. For this summary, recent insect activity is defined as any mountain pine beetle (MPB) or western spruce budworm (WSB) activity in any year prior to a given fire year (minimum 14, maximum 42 years). Data are individual fire years, log-transformed for display (constant value half the size of the smallest value in the dataset added to retain zeroes). See Table E1 (Appendix E) for values and number of fire years. Significant paired differences (Wilcoxon signed-rank test) indicated by asterisks (** = FDR-adjusted $P < 0.05$, * = FDR-adjusted $<$ 0.1). Orange asterisks denote positive differences; purple asterisks denote negative differences. See Appendix E: Tables E2 and E3 for additional details. Note that this figure excludes years with zero fire extent in both classes (at ecoregion scale), so the average annual fire likelihood values are lower than those displayed here. Note also that the Coast Range and Klamath Mountains ecoregions are excluded due to negligible insect activity, although they are included in the Forested Total category. Fire extent from perimeters (MTBS; 1984–2012; http://mtbs.gov) within forested ecoregion and state boundaries. Insect activity from aerial detection surveys (ADS; 1970–2012).

2011). Although important as landscape-scale fire events, these particular fire complexes appear to be exceptions to the general patterns exhibited across space and time.

DISCUSSION

Whereas previous research has focused on individual insect outbreaks or wildfires at finer
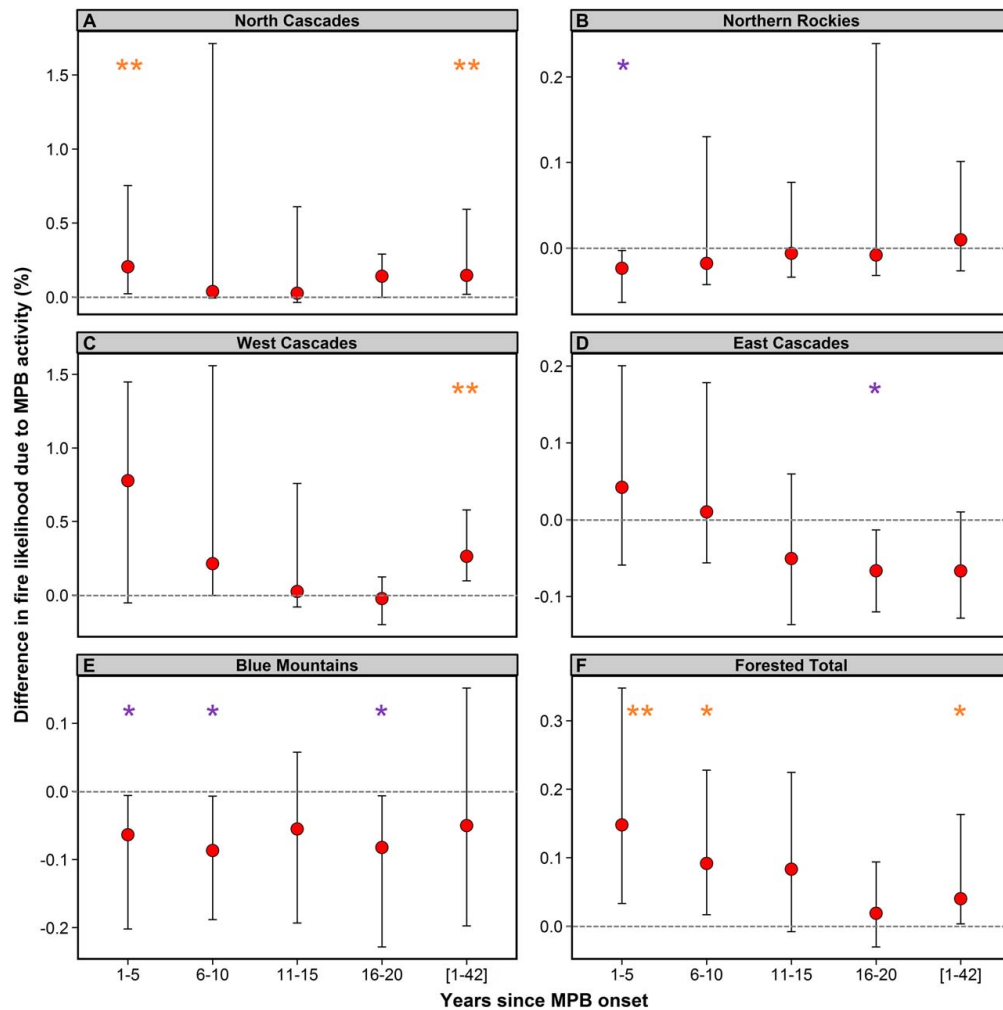
Fig. 4. Interannual differences in fire likelihood associated with mountain pine beetle (MPB) activity at recent time lags across forested ecoregions of the PNW. Intervals of insect onset are arranged with the most recent five year interval on the left and the interval of all available years on the right. Points are average differences (Wilcoxon signed-rank test pseudomedian). Error bars are nonparametric 95% confidence intervals. Significant paired differences indicated by asterisks (** = FDR-adjusted $P < 0.05$, * = FDR-adjusted < 0.1). Orange asterisks denote positive differences; purple asterisks denote negative differences. See Appendix E (Table E2) for additional details. Note that this figure excludes years without fire in both classes (at ecoregion scale) and that y-axes vary with ecoregion. Note also that the Coast Range and Klamath Mountains ecoregions are excluded due to negligible insect activity, although they are included in the Forested Total category. Fire extent from perimeters (MTBS; 1984–2012; http://mtbs.gov) within forested ecoregion and state boundaries. Insect activity from aerial detection surveys (ADS; 1970–2012).

scales, this study presents a novel, landscape- and regional-scale synthesis across numerous insect and fire events. Bark beetles, defoliators, and wildfires all influence PNW forests, but they may not overlap consistently enough to facilitate linked disturbance interactions as defined by Simard et al. (2011). Indeed, in recent decades across conifer forests of the PNW, there does not appear to be a consistent increase or decrease in wildfire likelihood following insect outbreaks.
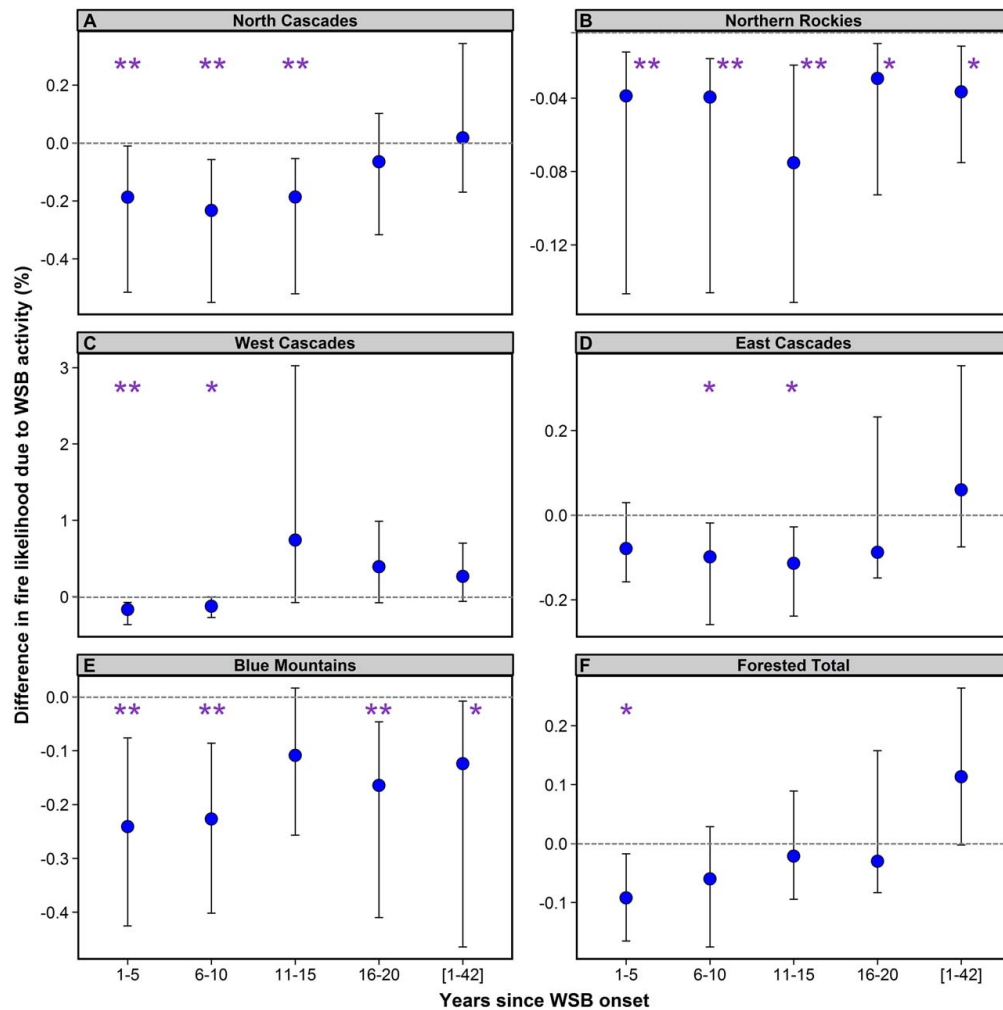
Fig. 5. Interannual differences in fire likelihood associated with western spruce budworm (WSB) activity at recent time lags across forested ecoregions of the PNW. Intervals of insect onset are arranged with the most recent five year interval on the left and the interval of all available years on the right. Points are average differences (Wilcoxon signed-rank test pseudomedian). Error bars are nonparametric 95% confidence intervals. Significant paired differences indicated by asterisks (** = FDR-adjusted $P < 0.05$, * = FDR-adjusted < 0.1). Orange asterisks denote positive differences; purple asterisks denote negative differences. See Appendix E (Table E3) for additional details. Note that this figure excludes years without fire in both classes (at ecoregion scale) and that y-axes vary with ecoregion. Note also that the Coast Range and Klamath Mountains ecoregions are excluded due to negligible insect activity, although they are included in the Forested Total category. Fire extent from perimeters (MTBS; 1984–2012; http://mtbs.gov) within forested ecoregion and state boundaries. Insect activity from aerial detection surveys (ADS; 1970–2012).

Interannual dynamics of bark beetles, defoliators, and wildfires across the PNW

As hypothesized, all three disturbance agents have occurred most prevalently in the drier, interior conifer forests east of the Cascade Crest. In general, native insect distributions match their host tree distributions, so it is not surprising that WSB has been the most extensive of the three disturbances (Fig. 2). Whereas MPB outbreaks are limited to areas with substantial lodgepole pine, WSB affects a variety of host tree species, including true firs, spruce, and Douglas-fir
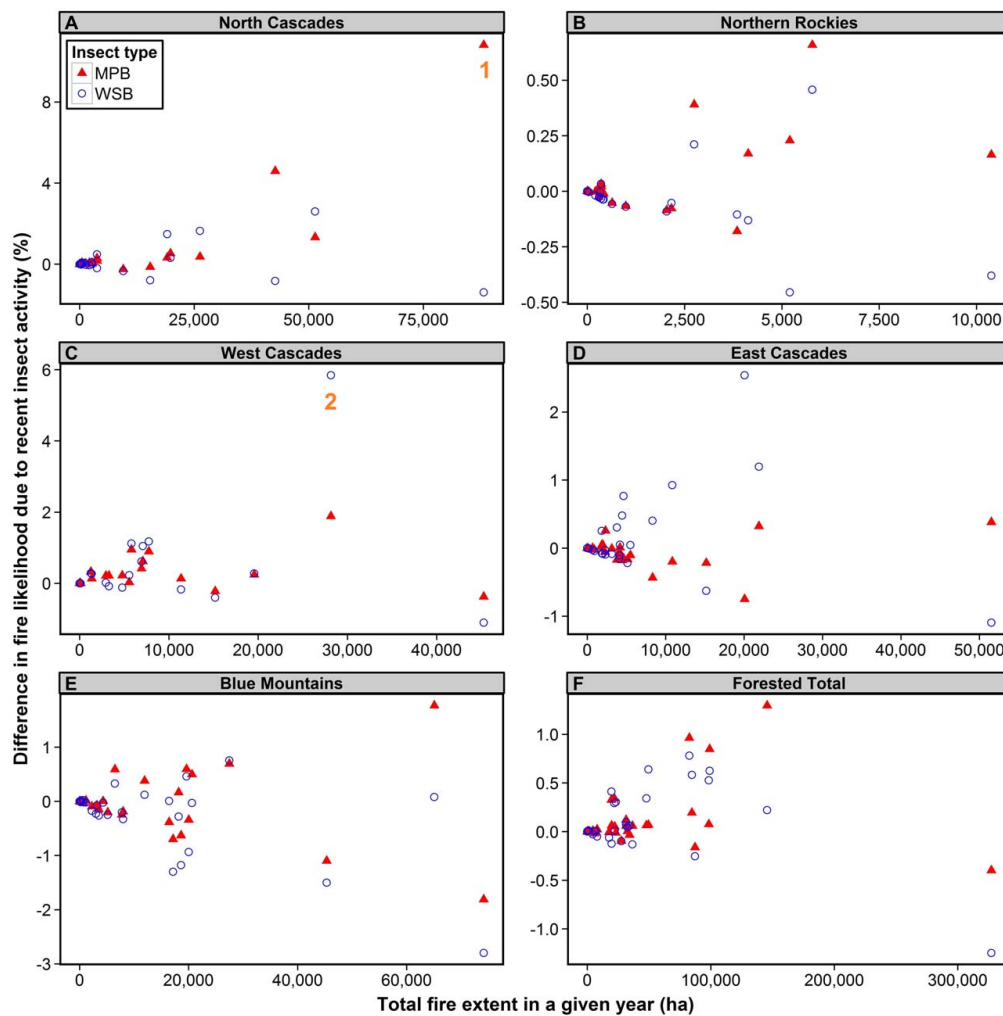
Fig. 6. Fire likelihood vs. interannual fire extent across forested ecoregions of the PNW affected by recent mountain pine beetle (MPB; red) and western spruce budworm (WSB; blue) activity (all years). Note that this plot excludes years with no area burned in both classes (at ecoregion scale). Note also that both the *x*- and *y*-axes vary among ecoregions and that the Coast Range and Klamath Mountains ecoregions are excluded due to negligible insect activity, although they are included in the Forested Total category. Fire extent from perimeters (MTBS; 1984–2012; http://mtbs.gov) within forested ecoregion and state boundaries. Insect activity from aerial detection surveys (ADS; 1970–2012; see *Methods*). Orange numbers denote specific fire complexes with high prevalence of prefire insect activity: 1: 2006 Tripod Fire (ca. 70,000 ha; Prichard and Kennedy 2014); 2: 2003 B&B Fire (ca. 37,000 ha; Crickmore 2011). See landscape maps in Appendix C.

(Furniss and Carolin 1977). Indeed, WSB has the potential to influence Douglas-fir forests throughout the western PNW but has been limited to drier, interior forests to date (Meigs et al. 2015).

In addition to affecting interior conifer forests, wildfire extended in an arc through the southwestern PNW region (Figs. 1 and 2). Notably, the

largest fire event in recent Oregon history—the Biscuit Fire, which burned ca. 10% of the Klamath Mountains ecoregion—occurred in an ecoregion with minimal influence from insect pests, including MPB and WSB. In most years, fire extent illustrates distinct temporal patterns among ecoregions, but 2002 stands out as a regional fire episode, consistent with climate-

driven synchrony (Heyerdahl et al. 2008).

Wildfire likelihood with and without recent insect activity

In general, although recent insect outbreaks peaked in years preceding most large fire years in the PNW (Fig. 2), wildfires are not consistently more or less likely in areas with prior insect activity (i.e., insect onset 14–42 years prefire). Thus, in contrast to our second hypothesis, insects and wildfires do not exhibit consistently linked disturbance interactions. Where insects and wildfires do co-occur, however, insect-fire likelihood appears to vary by insect type and ecoregion, with specific examples of higher fire likelihood following MPB outbreaks and lower fire likelihood following WSB outbreaks (Fig. 3). Importantly, all three disturbances are constrained spatially across forested ecoregions of the PNW (infrequently exceeding 2% of ecoregion extent in a given year; Fig. 2), indicating that there are large areas with neither insect nor wildfire throughout the study time period. This relative rarity means that even a strong causal relationship between insect-caused tree mortality and subsequent wildfire may not manifest itself at landscape or regional scales. Moreover, the relatively low fire likelihood in forests with or without prior insect activity reflects that wildfire is a relatively rare phenomenon, consistent with a general fire deficit relative to historic conditions (Marlon et al. 2012). Finally, the higher variability and negatively skewed distributions of fire likelihood in areas with recent insect activity (Fig. 3) are the result of multiple years without fire in insect-altered areas (i.e., because insects affect a small area in any given year relative to the available forest area; Fig. 2).

Insect-fire likelihood across different insect agents, time lags, ecoregions, and fire sizes

Our assessment of these insect-fire likelihood relationships at finer scales in both time (five year intervals) and space (ecoregions) illuminates more pronounced differences between areas with and without recent insect outbreaks (Figs. 4 and 5), supporting our third hypothesis and underscoring the key role of insect agent and time since outbreak (Hicke et al. 2012). For MPB, the five-year time lags reveal substantial variation, including inconsistent time lags for positive

linked effects, several examples of negative linked effects, and numerous time lag and ecoregion combinations without linked effects (Fig. 4). In contrast, more consistent patterns are evident for WSB, with examples of lower fire likelihood at multiple time lags in all ecoregions (Fig. 5). Thus, although both bark beetles and defoliators alter fuel profiles and associated fire potential at different time lags (e.g., Hummel and Agee 2003, Page and Jenkins 2007, Simard et al. 2011, Hicke et al. 2012, Donato et al. 2013), these windows of opportunity for increased or decreased fire likelihood are too narrow—and/or fire is too rare—for a uniform signal to emerge across PNW conifer forests.

There are individual fire years, however, with unusually strong positive insect-fire signals (e.g., 2006 in the North Cascades; Fig. 6A; Meigs 2014). These extreme positive years may be important examples of insect-fire co-occurrence at the small- to meso-landscape scale, resulting in compound disturbance effects even without broader evidence of linked disturbance effects (as in Harvey et al. [2013]). In addition, the lack of association between insect-fire likelihood and interannual fire extent (Fig. 6) suggests that the relationship between fire likelihood and prior insect activity is not more pronounced in mild, moderate, or extreme fire years. This result also suggests that other factors (such as climate; Heyerdahl et al. 2008) control the disproportionately large fire years accounting for the majority of regional fire extent (e.g., Strauss et al. 1989).

Our finding that insect-wildfire interactions appear to vary across insect agents, space, and time may help to reconcile divergent results in the literature. Looking across all possible years of prefire insect activity, we found examples of no difference in fire likelihood for each insect and in multiple ecoregions (Fig. 3), consistent with previous studies showing a lack of linked disturbance interactions (e.g., Kulakowski and Veblen 2007, Crickmore 2011, Harvey et al. 2013, Flower et al. 2014). Concurrently, specific examples of higher fire likelihood following MPB outbreaks (Figs. 3 and 5), driven in part by individual fires like the 2006 Tripod Fire, is consistent with studies showing positive linked interactions between MPB and the spatial patterns of fire at the event scale (Lynch et al. 2006, Prichard and Kennedy 2014). In addition, exam-

ples of both increased and decreased fire likelihood in locations with MPB activity in the prior five years (Fig. 4) partially supports results from a regional assessment of bark beetle-fire interactions that employed conditional probabilities similar to our fire likelihood indices but only up to five years prefire (Bisrat 2010). For WSB, lower fire likelihood across most ecoregions and time lags (Figs. 3 and 5) is consistent with findings of negative feedbacks between WSB and fire in British Columbia over the same general time period, perhaps due to canopy thinning and associated thickening of fire-resistant understory vegetation (Lynch and Moorcroft 2008). For the remaining ecoregions and time lags in our study, the lack of association between WSB and fire likelihood is consistent with a recent dendroecological assessment in the PNW (Flower et al. 2014). Finally, examples of higher fire likelihood following WSB activity in extreme years (Fig. 6) suggest that feedbacks and potential threshold effects between defoliators and wildfires merit further research.

Our empirical results are not directly comparable to studies that use simulation models to estimate fire behavior and/or effects in particular post-insect forest trees, stands, or landscapes (e.g., Hummel and Agee 2003, Page and Jenkins 2007, Simard et al. 2011, Cohn et al. 2014). These studies elucidate mechanistic relationships by assuming that a given insect-altered forest burns, whereas our findings suggest that, in any given year, fire influences a relatively small proportion of forests affected by insect activity (up to several decades earlier). Additional retrospective studies have used dendroecological methods, remote sensing, and landscape pattern analysis of individual fire events to assess the empirical evidence of insect-fire interactions over longer time periods (e.g., Bebi et al. 2003, Bigler et al. 2005, Kulakowski and Jarvis 2011). Although these studies have assessed non-MPB bark beetles or ecosystems outside of the PNW, our results are generally consistent with their findings of mixed or relatively weak feedbacks among insects and wildfires.

Uncertainties and future research

This study addresses insect-fire interactions at relatively broad landscape and regional scales, empirically quantifying wildfire likelihood across ecoregions where numerous fine-scale processes are operating, particularly forest management. Fire suppression/exclusion as well as thinning and/or salvage logging in MPB and WSB outbreak areas have been prevalent practices on public and private forests in recent decades (e.g., Sanders et al. 1985, Waring and Pitman 1985, Waring et al. 1992, Negron et al. 2008, Azuma 2010, Marlon et al. 2012), potentially altering the chance of fire encountering insect-altered forests and fuels. It is possible that insect and wildfire events would overlap more frequently in less intensively managed forests (i.e., wilderness areas) or in the future if climate change increases either disturbance (Heyerdahl et al. 2008, Kurz et al. 2008, Bentz et al. 2010, Littell et al. 2010). The relatively low fire likelihoods observed here (Fig. 3) would have to increase dramatically, however, to affect the amount of insect-fire overlap and associated evidence of linked disturbance interactions. Although fire extent has increased in recent decades, many forests in the PNW remain in a fire deficit relative to historic fire frequency and extent (e.g., Littell et al. 2009, Marlon et al. 2012). Furthermore, interannual climate is the most important top-down control of regional fire dynamics (Heyerdahl et al. 2008), and it appears that interannual fire extent is not associated with the fire likelihood differences between forests with and without prior insect activity (Fig. 6).

Additional uncertainties arise from limitations in the census data. The ADS data likely overestimate insect extent in some areas while simultaneously missing some insect impacts due to detectability challenges and spatial inaccuracies (Meddens et al. 2012, Meigs et al. 2015). The ADS polygons also encompass high heterogeneity in forest conditions and insect effects, and future studies could evaluate whether more constrained insect maps would yield different fire likelihood estimates, either focusing on higher damage ADS polygons or leveraging a more consistent change detection dataset like Landsat imagery (Meigs et al. 2015). Such a constrained approach may help to resolve the insect and non-insect components of our insect-fire likelihood matrix (Appendix D), but it would also reduce further any potential insect-fire overlap. Similarly, the MTBS fire perimeters contain a wide range of fire effects—including unburned or unburnable patches (Kolden et al. 2012)—that could mask potential

insect-fire signals. Future research could focus on how moderate- and high-severity fires are linked to insects and other potential drivers (e.g., climate; Kulakowski and Jarvis 2011). This approach, however, would also reduce potential insect-fire overlap and would require a severity classification scheme that is consistent across the full spectrum of forest types and prefire conditions in the region (e.g., the 685 fire polygons in our study). Future studies could also use ADS and MTBS data to investigate insect-fire interactions in other regions (e.g., US Rocky Mountains), although the ADS data may not be as spatiotemporally consistent (Meddens et al. 2012). Finally, although the Omernik (1987) level three ecoregions are very useful to assess broad landscape differences across the PNW, they encompass substantial variation in forest composition, structure, and disturbance history. All three of these factors are important for MPB, WSB, and wildfire behavior and effects (e.g., Sanders et al. 1985, Hessburg et al. 2000, Raffa et al. 2008). It is possible that summaries based on finer-grained vegetation maps (such as potential vegetation type; [Henderson et al. 2011] or imputation-based attributes [Ohmann et al. 2012]), would yield different or more context-specific results. Future studies could focus on finer-scale patterns of host tree distributions, fuel conditions, and drought stress within specific ecoregions or management units (e.g., national forests) of interest, albeit with a narrower scope than the current study.

Similarly, although our census data cover a relatively large number of fires (beginning in 1984) and insect outbreaks (beginning in 1970), future studies could account for longer time periods, additional disturbance agents, and other response variables. For example, bark beetles have been shown to double coarse fuels 25–30 years post-outbreak (Donato et al. 2013), but we limited our time lag analysis to 20 years to retain balance in our fire sample. Indeed, longer-term records—if such spatially extensive datasets were available—would enable the investigation of potential spatiotemporal linkages among insects and wildfires operating under historic climate and disturbance regimes (e.g., Flower et al. 2014). There are inherent tradeoffs, however, between temporally rich, spatially limited datasets like tree rings and the

temporally limited, spatially rich remote sensing data used here. In addition, PNW forests are influenced by numerous, interacting biotic and abiotic disturbance factors, including other insects (e.g., fir engraver beetle [*Scolytus ventralis* LeConte {Coleoptera: Curculionidae: Scolytinae}], Douglas-fir tussock moth [*Orgyia pseudotsugata* {McDunnough} {Lepidoptera: Lymantriidae}]; Furniss and Carolin 1977), diseases, drought, storms, logging, and grazing. These factors contribute to the variation in our fire likelihood results, but the net effect remains a lack of insect-fire overlap across the forest landscapes and time periods we assessed.

Even where insects and wildfires do overlap in space and time, it would be informative to distinguish the overlap that would be expected given other covarying drivers. Indeed, the three disturbances we assessed are catalyzed by the same abiotic and biotic factors (e.g., drought, tree composition, structure, and vigor, and landscape contiguity; Kulakowski and Jarvis 2011, Meigs et al. 2011, Simard et al. 2011, Prichard and Kennedy 2014), and future studies could quantify these drivers explicitly, further clarifying mechanistically linked interactions from coincident interactions. Future research also could investigate the interactions between insect outbreaks and fire severity rather than likelihood, focusing only on fires with substantial prior insect activity, a small subset of fire events representing a high research and management priority.

Management implications

Our central finding that wildfire likelihood does not consistently increase or decrease in areas affected by recent insect outbreaks has several important implications for forest management. First, although relatively rare in any given year or ecoregion (Fig. 2), each of the three disturbances—MPB, WSB, and wildfire—will continue to influence PNW forests, and it may be efficient to focus on their individual forest health impacts more than their interactions. Because these disturbances are not distributed evenly across space and time, it also makes sense to prioritize management activities on specific landscapes with higher disturbance impacts and/ or more valuable ecosystem services. For example, portions of the North Cascades and West

Cascades ecoregions have experienced recent pulses of all three disturbances (Figs. 1 and 2) as well as substantial insect-fire overlap events (Appendix C). These regional disturbance hotspots represent an opportunity to study and adaptively manage for resilience, particularly when these disturbances occur outside of wilderness areas, where management options are limited.

Second, when and where wildfires do occur in recent or ongoing insect outbreaks, fire behavior and effects may change (e.g., higher rate of spread or severity; Perrakis et al. 2014, Prichard and Kennedy 2014), fire management will likely be more challenging (Hicke et al. 2012, Page et al. 2013), and compound disturbance effects must be addressed (e.g., Harvey et al. 2013). Because fire and insect likelihood are generally low (Fig. 3), however, strategic plans should recognize that these compound disturbances are relatively rare across time and space. Moreover, our finding that WSB outbreaks are associated with decreased fire likelihood suggests that these defoliators may function as forest thinning agents, potentially benefiting ecosystem restoration and fuel reduction strategies. In addition, both MPB and WSB are native to PNW forests and likely contribute to the pyrodiversity (Martin and Sapsis 1991) inherent to mixed-severity fire regimes. Because these insects may not represent a regional forest health crisis, there are likely higher priorities for ecosystem restoration programs, such as fuel and fire dynamics at the wildland-urban interface.

Third, forests will continue to burn whether or not there was prior insect activity, and known fire drivers like fuel accumulation and vegetation stress likely will play a more important role in a warmer, potentially drier future (McKenzie et al. 2004, Westerling et al. 2006, Heyerdahl et al. 2008, Littell et al. 2010). Long-term adaptive management approaches will remain essential, and it is imperative that programs like the ADS and MTBS continue to track these disturbances with consistent protocols and accessible data. Given societal concerns about forest health in a rapidly changing world, ongoing research and monitoring will enable forest managers to quantify and anticipate the independent and interactive effects of insects, wildfires, and other disturbances, both native and novel.

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Supplemental Material

Appendix A

Table A1. Glossary of abbreviations used in the text.

Abbreviation	Description
ADS	Aerial detection survey
FDR	False discovery rate
GDAL	Geospatial Data Abstraction Library
IDL	Interactive data language
MPB	Mountain pine beetle (*Dendroctonus ponderosae* Hopkins [Coleoptera: Curculionidae: Scolytinae])
MTBS	Monitoring Trends in Burn Severity
NLCD	National Land Cover Database
PNW	US Pacific Northwest (Oregon and Washington)
SR	Wilcoxon signed-rank test
USGS GAP	United States Geological Survey Gap Analysis Program
WSB	Western spruce budworm (*Choristoneura freemani* Razowski [Lepidoptera: Tortricidae])

Appendix B

Table B1. Spatial extent of generally forested ecoregions in the PNW study area.

Forested ecoregion†	Total extent (ha)	Forest extent (ha)‡	Forest extent (%)
Blue Mountains	6,408,121	3,586,796	56
Coast Range	4,040,664	3,684,222	91
East Cascades	3,563,709	2,846,506	80
Klamath Mountains	1,567,722	1,352,716	86
Northern Rockies	2,144,102	1,527,448	71
North Cascades	3,033,832	2,578,162	85
West Cascades	4,495,419	4,246,610	94
Total	25,253,569	19,822,461	78

Note: This table corresponds to the study area map in Fig. 1.
  † We include only the generally forested ecoregions (Omernik 1987).
  ‡ We limit the fire likelihood analysis to forested areas using a forest mask based on USGS GAP and NLCD maps (30-m grain; Ohmann et al. 2012; data available online: http://gapanalysis.nbii.gov/, http://landcover.usgs.gov/).

APPENDIX C
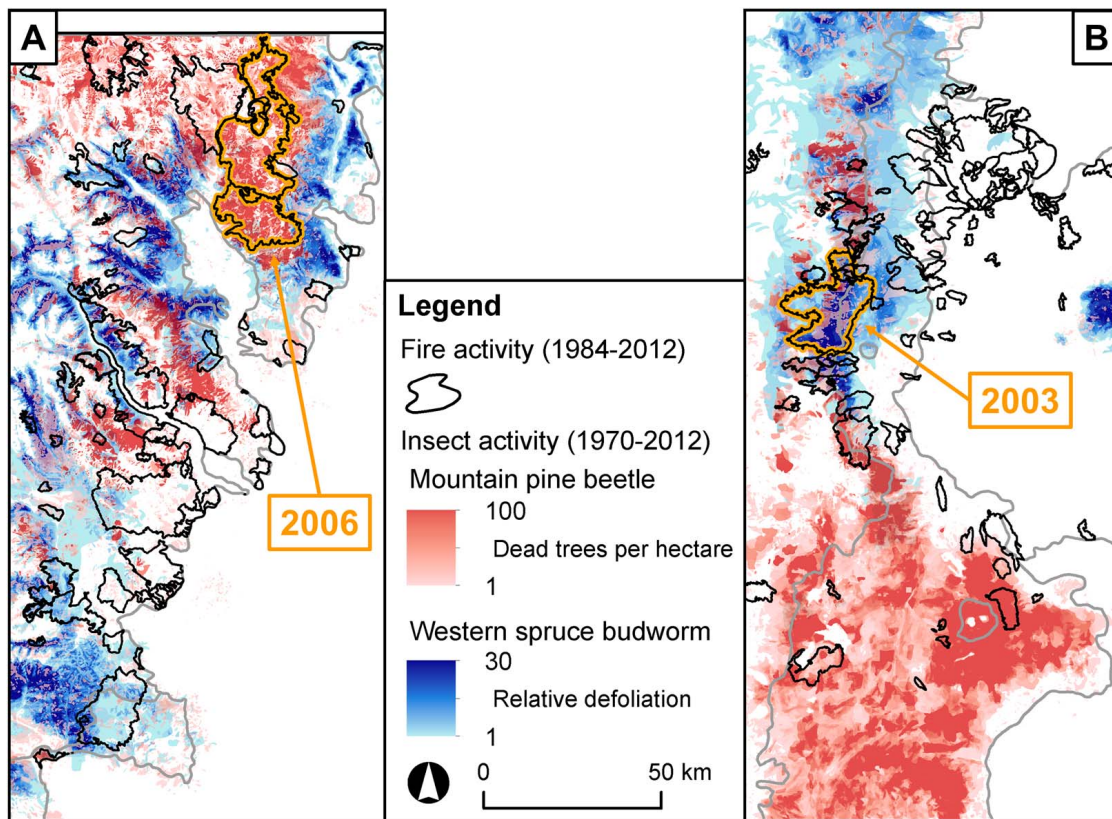
Fig. C1. Distribution of insects and wildfires across example landscapes in the North Cascades of WA (A) and West and East Cascades of OR (B; locations and ecoregions denoted in Fig. 1). Fire perimeters (MTBS; 1984–2012; http://mtbs.gov) are clipped within forested ecoregion and state boundaries. Cumulative insect activity from aerial detection surveys (ADS; 1970–2012; see *Methods*). Note that mountain pine beetle (MPB; red) overlaps western spruce budworm (WSB; blue) activity in this display (MPB shown with 30% transparency), revealing purple locations with both insects. Orange perimeters denote specific fire complexes with high prevalence of prefire insect activity: 2006 Tripod Fire (ca. 70,000 ha; Prichard and Kennedy 2014); 2003 B&B Fire (ca. 37,000 ha; Crickmore 2011).

Appendix D

Fig. D1. Two-way insect-fire likelihood matrix, where the empirical wildfire likelihood index is expressed as the percent burned of the area available in a given year. Fire likelihood in areas with prior insect activity: FL_I: $A/(A + B) \times 100$. Fire likelihood in areas without prior insect activity: FL_{NI}: $C/(C + D) \times 100$.

APPENDIX E

Table E1. Insect-fire likelihood across forested ecoregions affected by recent insect activity.

Ecoregion†	No. fire years‡	Insect§	Fire type¶	FL# (min)‖	FL (25%)††	FL (median)‡‡	FL (75%)††	FL (max)‖	FL (mean)
North Cascades	21	MPB	Prior insect	0.000	0.029	0.138**	0.996	1.337	1.265
			No prior insect	0.000	0.015	0.093**	0.669	1.501	0.397
		WSB	Prior insect	0.000	0.015	0.097	0.999	2.381	0.647
			No prior insect	0.000	0.018	0.097	0.606	1.339	0.499
Northern Rockies	21	MPB	Prior insect	0.000	0.013	0.040	0.119	0.119	0.173
			No prior insect	0.001	0.018	0.031	0.152	0.298	0.116
		WSB	Prior insect	0.000	0.000	0.000*	0.089	0.177	0.092
			No prior insect	0.001	0.025	0.038*	0.159	0.308	0.133
West Cascades	16	MPB	Prior insect	0.001	0.233	0.359**	0.722	0.995	0.567
			No prior insect	0.003	0.047	0.105**	0.288	0.511	0.213
		WSB	Prior insect	0.000	0.054	0.280	0.806	1.233	0.748
			No prior insect	0.000	0.046	0.076	0.162	0.283	0.187
East Cascades	24	MPB	Prior insect	0.000	0.043	0.090	0.177	0.311	0.226
			No prior insect	0.000	0.049	0.178	0.309	0.642	0.293
		WSB	Prior insect	0.000	0.000	0.059	0.544	1.093	0.397
			No prior insect	0.000	0.046	0.104	0.173	0.231	0.217
Blue Mountains	28	MPB	Prior insect	0.000	0.003	0.073	0.577	1.214	0.371
			No prior insect	0.001	0.028	0.205	0.539	1.197	0.421
		WSB	Prior insect	0.000	0.009	0.091*	0.418	0.726	0.298
			No prior insect	0.000	0.041	0.267*	0.613	1.309	0.579
Forested Total	28	MPB	Prior insect	0.000	0.060	0.187*	0.387	0.590	0.360
			No prior insect	0.000	0.049	0.141*	0.241	0.489	0.223
		WSB	Prior insect	0.000	0.039	0.213	0.551	1.031	0.331
			No prior insect	0.000	0.046	0.130	0.218	0.377	0.223

Notes: This table corresponds directly to boxplots in Fig. 3.

† We include only forested ecoregions (Omernik 1987) with substantial MPB or WSB activity (1970–2012, from ADS). Forested total includes the ecoregions shown here plus the Coast Range and Klamath Mountains, which are otherwise excluded due to minimal insect activity.

‡ We exclude years with no fire in a given ecoregion.

§ MPB: mountain pine beetle; WSB: western spruce budworm.

¶ Fire type: with or without insect activity in all years preceding a given fire year (Appendix D).

FL: Fire likelihood based on percent burned of available area and calculated with two-way likelihood matrix (Appendix D).

‖ Minimum and maximum values correspond to end of boxplot vertical lines (Fig. 3) and do not include outliers.

†† The 25% and 75% quartiles correspond to the outside edges of the boxplots (Fig. 3).

‡‡ Significant paired differences (Wilcoxon signed-rank test) indicated asterisks at two FDR-adjusted α levels (* indicates FDR-adjusted $P < 0.1$; ** indicates FDR-adjusted $P < 0.05$). See Tables E2 and E3 for additional details.

Table E2. Statistical summary of paired differences in insect-fire likelihood across forested ecoregions affected by recent mountain pine beetle (MPB) activity at different time lags.

Ecoregion†	No. fire years‡	Time lag§	Difference (median)¶	Difference (95% CI)#	P
North Cascades	21	1–5	0.204	0.022 to 0.753	0.046
	21	6–10	0.037	−0.007 to 1.712	0.246
	21	11–15	0.026	−0.036 to 0.609	0.649
	17	16–20	0.140	−0.002 to 0.290	0.110
	21	All (1–42)	0.145	0.019 to 0.592	0.046
Northern Rockies	21	1–5	−0.024	−0.064 to −0.003	0.085
	21	6–10	−0.018	−0.043 to 0.130	0.277
	21	11–15	−0.006	−0.034 to 0.077	0.663
	19	16–20	−0.008	−0.032 to 0.239	0.588
	21	All (1–42)	0.009	−0.027 to 0.101	0.706
West Cascades	16	1–5	0.777	−0.053 to 1.449	0.216
	16	6–10	0.213	−0.003 to 1.559	0.105
	16	11–15	0.024	−0.081 to 0.759	0.756
	14	16–20	−0.024	−0.201 to 0.123	0.705
	16	All (1–42)	0.263	0.097 to 0.579	0.046
East Cascades	24	1–5	0.042	−0.059 to 0.200	0.478
	24	6–10	0.010	−0.056 to 0.178	0.812
	24	11–15	−0.051	−0.137 to 0.060	0.517
	20	16–20	−0.067	−0.120 to −0.013	0.068
	24	All (1–42)	−0.067	−0.128 to 0.010	0.163
Blue Mountains	28	1–5	−0.064	−0.202 to −0.006	0.073
	28	6–10	−0.087	−0.188 to −0.007	0.065
	28	11–15	−0.055	−0.193 to 0.058	0.170
	23	16–20	−0.082	−0.228 to −0.007	0.069
	28	All (1–42)	−0.050	−0.197 to 0.152	0.345
Forested Total	28	1–5	0.148	0.033 to 0.348	0.047
	28	6–10	0.091	0.017 to 0.228	0.068
	28	11–15	0.083	−0.008 to 0.225	0.173
	23	16–20	0.019	−0.030 to 0.094	0.589
	28	All (1–42)	0.040	0.003 to 0.163	0.072

Notes: This table corresponds directly to Fig. 4. We assess paired differences with the Wilcoxon signed-rank test because it is robust to skewed distributions (see *Methods*).

† We include only forested ecoregions (Omernik 1987) with substantial MPB or WSB activity (1970–2012, from ADS). Forested total includes the ecoregions shown here plus the Coast Range and Klamath Mountains, which are otherwise excluded due to minimal insect activity.

‡ Number of years is reduced for the longest time lag we assessed because the earliest fire year in that subset is 1990.

§ Time lags represent the years since first aerial survey observation of insect activity.

¶ Pseudomedian of the paired difference in fire likelihood with and without prior insect activity.

\# Nonparametric confidence interval calculated after Bauer (1972).

Table E3. Statistical summary of paired differences in insect-fire likelihood across forested ecoregions affected by recent western spruce budworm (WSB) activity at different time lags.

Ecoregion†	No. fire years‡	Time lag§	Difference (median)¶	Difference (95% CI)#	P
North Cascades	21	1–5	−0.187	−0.516 to −0.011	0.049
	21	6–10	−0.233	−0.550 to −0.057	0.003
	21	11–15	−0.187	−0.520 to −0.054	0.003
	17	16–20	−0.065	−0.317 to 0.102	0.265
	21	All (1–42)	0.018	−0.170 to 0.344	0.705
Northern Rockies	21	1–5	−0.039	−0.147 to −0.015	0.029
	21	6–10	−0.040	−0.146 to −0.018	0.021
	21	11–15	−0.075	−0.151 to −0.022	0.001
	19	16–20	−0.029	−0.093 to −0.010	0.064
	21	All (1–42)	−0.037	−0.075 to −0.012	0.064
West Cascades	16	1–5	−0.167	−0.366 to −0.076	0.014
	16	6–10	−0.126	−0.273 to −0.003	0.095
	16	11–15	0.740	−0.077 to 3.025	0.505
	14	16–20	0.392	−0.079 to 0.988	0.183
	16	All (1–42)	0.266	−0.062 to 0.701	0.170
East Cascades	24	1–5	−0.079	−0.158 to 0.030	0.163
	24	6–10	−0.098	−0.259 to −0.019	0.069
	24	11–15	−0.114	−0.238 to −0.028	0.050
	20	16–20	−0.088	−0.148 to 0.232	0.138
	24	All (1–42)	0.060	−0.075 to 0.353	0.702
Blue Mountains	28	1–5	−0.241	−0.425 to −0.076	0.001
	28	6–10	−0.227	−0.402 to −0.086	0.001
	28	11–15	−0.109	−0.257 to 0.016	0.138
	23	16–20	−0.164	−0.410 to −0.046	0.010
	28	All (1–42)	−0.124	−0.464 to −0.008	0.064
Forested Total	28	1–5	−0.092	−0.165 to −0.017	0.064
	28	6–10	−0.060	−0.175 to 0.029	0.255
	28	11–15	−0.021	−0.094 to 0.089	0.682
	23	16–20	−0.030	−0.083 to 0.158	0.345
	28	All (1–42)	0.113	−0.002 to 0.264	0.110

Notes: This table corresponds directly to Fig. 5. We assess paired differences with the Wilcoxon signed-rank test because it is robust to skewed distributions (see *Methods*).

† We include only forested ecoregions (Omernik 1987) with substantial MPB or WSB activity (1970–2012, from ADS). Forested total includes the ecoregions shown here plus the Coast Range and Klamath Mountains, which are otherwise excluded due to minimal insect activity.

‡ Number of years is reduced for the longest time lag we assessed because the earliest fire year in that subset is 1990.

§ Time lags represent the years since first aerial survey observation of insect activity.

¶ Pseudomedian of the paired difference in fire likelihood with and without prior insect activity.

Nonparametric confidence interval calculated after Bauer (1972).