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Disturbance, tree mortality, and implications for contemporary regional forest change in the Pacific Northwest

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ABSTRACT

Tree mortality is an important demographic process and primary driver of forest dynamics, yet there are relatively few plot-based studies that explicitly quantify mortality and compare the relative contribution of endogenous and exogenous disturbances at regional scales. We used repeated observations on 289,390 trees in 3673 1 ha plots on U.S. Forest Service lands in Oregon and Washington to compare distributions of mortality rates among natural disturbances and vegetation zones from the mid-1990s to mid-2000s, a period characterized by drought, insect outbreaks, and large wildfires. Endogenous disturbances (e.g. pathogens, insects) were pervasive but operated at relatively low levels of mortality (<2.5%/yr) that rarely exceeded 5%/yr. Exogenous disturbances (e.g. fire, wind, landslides, avalanches) were less common and operated mostly at intermediate levels of mortality (5–25%/yr) indicative of partial-stand-replacement events. Stand-replacing mortality rates (⩾25%/yr) comprised a third of all exogenous disturbance events, occurring almost exclusively in fires. Fires were rare in wet vegetation zones and most rates were <2.5%/yr and associated with endogenous processes. Mortality rates in dry vegetation zones revealed a different set of dynamics including a more variable role of background mortality and greater proportions of mortality associated with fire and insects at partial- and stand-replacing levels. Mortality rates in early and middle stages of stand development were low compared to published rates, but rates >1%/yr in over half of the plots in late and old-growth stages corroborate previous findings of elevated mortality during the same period and indicate the potential for pervasive structural change across all vegetation zones. Partial- and stand-replacing fire were associated with most mortality, but affected a relatively small proportion of dry vegetation zones (3.1–7.1% and 2.1–5.1%, respectively). These disturbances have likely affected regional biodiversity through the creation of early seral habitat, increased within-stand heterogeneity, and restored some aspects of historical fire regimes, but there is a need to better understand corresponding structural and compositional changes. We demonstrate the variability in the drivers, magnitude, and extent of mortality across a biophysically diverse region and highlight the need to incorporate and characterize the effects of mortality at intermediate levels to develop a more comprehensive understanding of regional forest dynamics.

1. Introduction

Tree mortality is an important demographic process (Harcombe, 1987) and primary driver of the structure, composition, and function of forested ecosystems (Franklin et al., 1987). Increasing "background" mortality rates (van Mantgem et al., 2009; Peng et al., 2011; Luo and Chen, 2013), widespread mortality events (e.g. Allen et al., 2010), and altered disturbance regimes associated with a changing climate indicate an increasing role of mortality in forests across the globe (Dale et al., 2001; Seidl et al., 2014). Despite this, the relative contribution of endogenous biotic disturbances (e.g. pathogens, insects) and exogenous physical disturbances (e.g. fire, wind, landslides, floods, avalanches) (White, 1979) and how they vary at a regional scale are largely unknown. Coarse-scale exogenous disturbances are hypothesized to drive as much or more of forest dynamics as fine-scale endogenous processes (Spies and Franklin, 1989), but there is little empirical data that quantifies mortality as a demographic rate and compares among disturbance agents and biophysical settings at a regional scale. Such knowledge is needed to quantify the magnitude and extent of mortality induced ecological change and to provide a solid spatial and temporal context for future comparisons among other regions.

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Most demographic studies of tree mortality focus on background mortality associated with endogenous processes originating internally from within a stand. These include density-dependent thinning (Lutz and Halpern, 2006), senescence of older trees, crushing and physical damage (Clark and Clark, 1991; Larson and Franklin, 2010), and biotic disturbances including endemic pathogen and insect activity (e.g. van Mantgem et al., 2009) (Fig. 1). Background mortality operates continuously at fine scales and ultimately drives long-term patterns of development in many forested ecosystems (Franklin et al., 2002). Insects and pathogens are considered endogenous disturbances, but epidemic outbreaks triggered by drought have affected large spatial extents across the western United States (Logan et al., 2003; Raffa et al., 2008; Williams et al., 2010) and are predicted to be exacerbated by future climate change (Dale et al., 2001). Recent advances in remotely-sensed applications have reduced uncertainties in aerial detection survey data (ADS) and refined estimates of mortality (Meddens et al., 2012; Meigs et al., 2015), but plot-based studies quantifying mortality as a demographic rate are limited in the western United States to a few studies based on observations on a few species (Shaw et al., 2005) or single vegetation zone (Ganey and Vojta, 2011).

Background mortality is a valuable concept and provides a baseline to compare with future changes, but does not account for the variety of natural exogenous disturbances operating across a regional extent. Traditional conceptual models of forest structural development (e.g. Oliver and Larson, 1990; Franklin et al., 2002) and landscape dynamics (e.g. Turner et al., 1993) characterize exogenous disturbances such as fire, wind, landslides, and avalanches as stand-replacing events that re-initiate dynamics. However, exogenous disturbances have a range of effects on ecosystems (see White, 1979) which are not necessarily catastrophic in an ecological sense (Keane et al., 2009). The local-scale infrequency and unpredictability of exogenous disturbances make plot-based studies quantifying tree mortality difficult and replication across multiple events with pre-disturbance data are rare (Turner and Dale, 1998). Thus, the actual distributions of mortality rates associated with exogenous disturbances are largely unknown for any region. Remote sensing-based studies have identified wildfires as a major driver of regional forest change (e.g. Williams et al., 2010; Cansler and McKenzie, 2014), but are generally limited to broad classes of severity and lack the ecological resolution capable of capturing demographic measures of mortality provided by repeated measure plot studies.

We used repeat observations from 3673 forest inventory plots distributed in a systematic sampling design across 11 million ha of US Forest Service lands in the Pacific Northwest to examine variation in short interval (4–10 years) stand-level rates of tree mortality from the mid-1990s to the mid-2000s. Our study period coincides with the warmest decade the study region has experienced since the start of the 20th century (Abatzoglou et al., 2014) accompanied by increasing background mortality rates in old-growth forests (van Mantgem et al., 2009), widespread insect activity (Meigs et al., 2015), and an increase in area burned by wildfire (Littell et al., 2009). We address three questions: (1) What is the relative contribution of endogenous and exogenous disturbances to the regional scale distribution of mortality rates, (2) how do distributions of mortality rates differ among endogenous and exogenous disturbance agents, and (3) how do distributions of mortality rates differ among vegetation zones?

2. Methods

2.1. Study region

Our study region is approximately 11 million ha and includes all lands administered in Oregon and Washington by the US Forest Service (Fig. 2). The region is highly diverse and includes a variety of potential vegetation types due to strong climatic and topographic gradients (Franklin and Dyrness, 1973) (Fig. 2). We acquired a map of potential vegetation zones created using existing forest inventory data on species distributions in relation to dominant climatic and topographic gradients (Henderson et al., 2011) from the Ecoshare Interagency Clearinghouse of Ecological Information (www.ecoshare.info/category/gis-data-vegzones). Vegetation zones represent biophysical environments and geographic ranges distinguished by the tree species that would dominate in later developmental stages in the absence of stand replacing disturbance (Pfister and Arno, 1980). Wet vegetation zones include western hemlock (*Tsuga heterophylla*), silver fir, (*Abies amabilis*), and mountain hemlock (*Tsuga mertensiana*). Dry vegetation zones include ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Psuedotsuga*

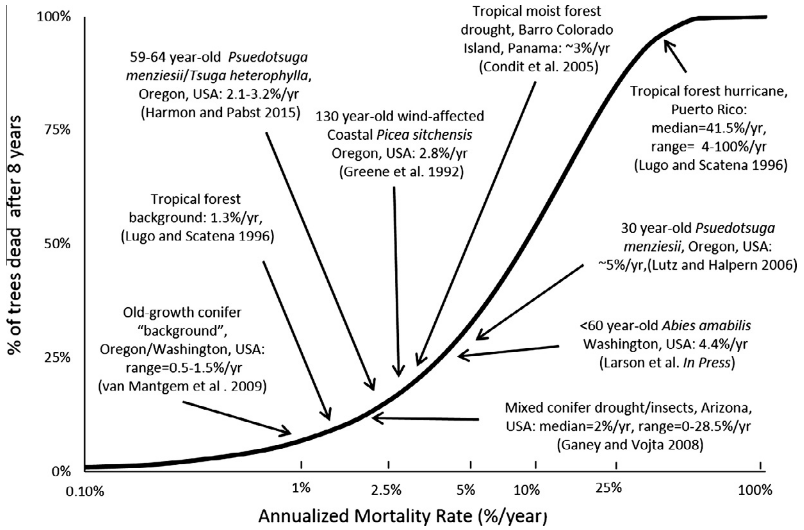

Fig. 1. Cumulative percent of trees dying after eight years at corresponding stand mortality rates along with published mortality rates from selected studies. Demographic studies of tree mortality annualize mortality rates as study intervals often vary. Thus, a mortality rate of 10%/yr over an eight year period corresponds with mortality of approximately 50% of all trees while a rate of 25%/yr is essentially "stand-replacing" with approximately 75% of all trees dying. (See above-mentioned references for further information.)

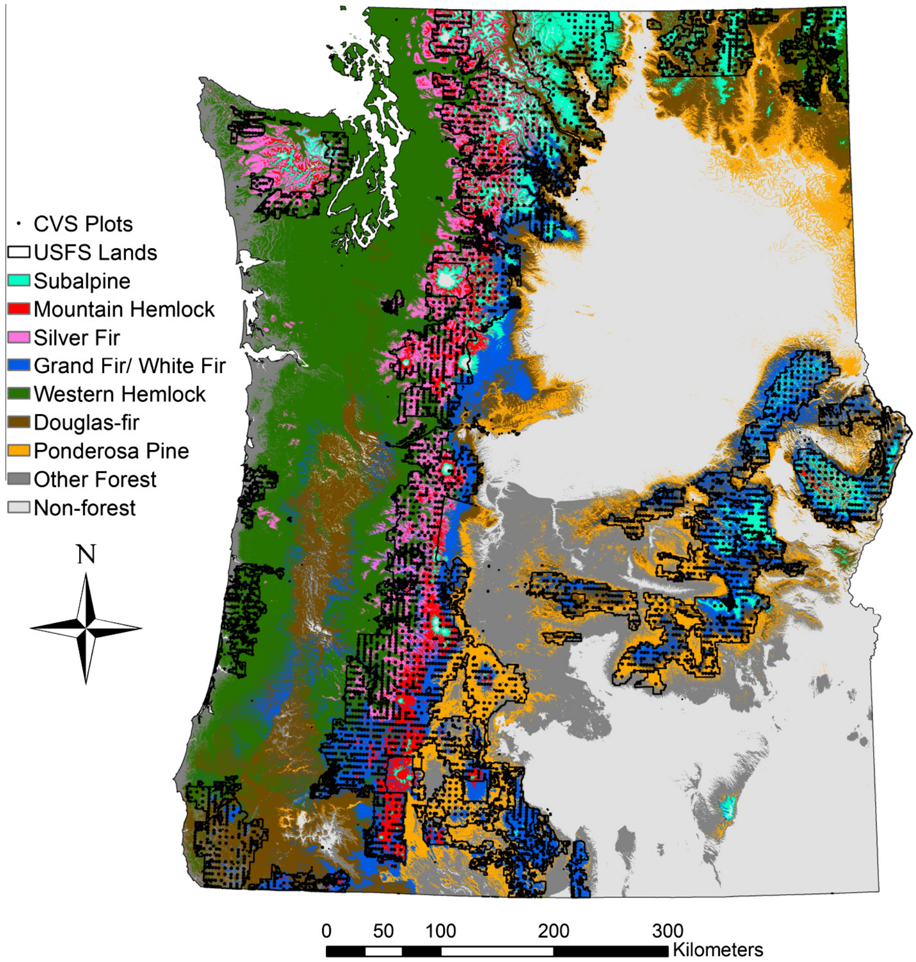

Fig. 2. Potential vegetation zones of the Pacific Northwest (Henderson et al., 2011) with boundaries of USFS lands and approximate locations of 3673 Current Vegetation Survey plots.

menziesii), grand fir/white fir (*Abies grandis Abies concolor*), and subalpine which includes subalpine fir (*Abies lasiocarpa*) and parklands dominated by whitebark pine (*Pinus albicaulis*).

A variety of natural and anthropogenic disturbances influenced the development of forest structure in all vegetation zones, most of which are composed of forests in mature, late, and old-growth stages of structural development (Reilly and Spies, 2015). Wildfire played a major role across the entire study region during different time periods (Weisberg and Swanson, 2003; Heyerdahl et al., 2008). Historic fire regimes range from high frequency, low severity fire in warm, dry forests to low frequency, high severity fire on cold and wet forests, but much of the vegetation in the region was historically subject to large fires and a mixed severity fire regime where the proportion of high severity fire varied spatially and temporally (Agee, 1993). Long periods of fire exclusion are believed to have altered forest composition and structure in dry forests of the eastern and southern portions of the region (Perry et al., 2011), but wildfires have increased in frequency and extent since the mid-1950s (Littell et al., 2009). Windstorms and landslides associated with storms off the Pacific Ocean also play a greater role closer to the coast and on exposed landforms (Sinton et al., 2000).

2.2. Field data

We acquired field data from the Current Vegetation Survey (CVS) inventory of USDA Forest Service Pacific Northwest Region 6 (Max et al., 1996). The CVS is a precursor to the Forest Inventory and Analysis (FIA) program. Plots are located on a systematic 2.74 km by 2.74 km grid across all the national forest lands in Oregon and Washington, with the exception of federally designated wilderness areas where plots are located every 5.74 km (Fig. 2). Forest Service lands comprise over half of the forested portion of the region and have good geographic coverage of most vegetation zones with the exception of western hemlock which is primarily under private ownership. Our sample in this vegetation zone is mostly limited to parts of the Coast Range and the southern portion of the Western Cascades of Oregon. With the exception of the Olympic Peninsula in the northwestern part of the region, higher elevation silver fir and mountain hemlock vegetation zones are well represented in our sample. Dry vegetation zones are well represented geographically in our sample with the exception of Douglas-fir in the southwestern portion of the region and ponderosa pine and Douglas-fir in the northeastern part of the region.

The CVS plot design includes five sets of nested fixed-radius subplots located within a circular 1 ha plot with one set of subplots located at plot center and the other four sets of subplot centers located 40.8 m away in each of the four cardinal directions. Trees in different size classes were sampled within each fixed-radius subplot according to the following: 2.5–7.5 cm dbh (0.004 ha), 7.6–32.9 cm dbh (0.02 ha), and ⩾33 cm (0.075 ha). In plots west of the Cascade Crest all trees ⩾122 cm dbh were measured across the entire hectare. Trees in different size classes were expanded based on subplot size to provide an estimate of the number of live trees per hectare. East of the Cascade Crest, all trees ⩾76 cm were measured across the entire hectare. All live trees were tagged at breast height (1.37 m) and measured for diameter between 1992 and 1997. Plots were measured again between 1997 and 2007 and previously tagged trees were re-measured and recorded as live or dead. We limited our sample to plots with ⩾20 live trees, intervals ⩾4 years and <10 years between sampling (mean = 7.9 years), and no evidence of logging or human related mortality during the interval to limit potential sources of mortality to natural causes. We used data from 3673 plots with 289,390 tagged trees.

We used narratives written at plot installation and re-measurement on present conditions and past disturbance (PCPD) to document the occurrence of specific disturbances during the interval. Protocol explicitly included documenting the occurrence of disease/pathogens, insects, wind, and fire, but avalanches, flooding, and landslides were also documented. Reference to disturbance was recorded as a presence/absence indicator of disturbance occurrence with no interpretation of severity to avoid field recorder bias. Our goal was not specifically attributing mortality to any single disturbance agent or distinguishing between proximate and ultimate causes of mortality, but rather to document the range of mortality levels across which individual and multiple disturbances occur. In instances when multiple disturbances were recorded, we used details in the field notes to attribute the dominant disturbance. We are thus confident in attributing a dominant disturbance when mortality was high, but there is likely some misclassification at low levels of mortality where multiple disturbances were recorded. We use plots with no recorded disturbance as a baseline distribution to compare to those of individual disturbances, while plots with multiple disturbances (e.g. insects/pathogens and fire/insects) may be compared to that of individual agents to understand how the occurrence of multiple disturbances may shift the distribution of mortality rates.

We used randomForest (R version 2.13.2) to classify plots into a pre-existing classification of forest structure based live tree biomass, density and tree size, abundance of dead wood, and understory cover (Reilly and Spies, 2015) with an overall error rate of 20.5%. Plots were then binned into stages of development (early, mid, mature, or late/old-growth) based on live biomass, canopy cover, maximum tree size, number of big trees, biomass of snags and dead wood, age, and disturbance history. We chose to base these stages on structure because age is a poor surrogate for forest development in dry vegetation zones where disturbance regimes include low-severity or partial stand-replacing disturbance and age structure is far more complex (Muir, 1993; Taylor and Skinner, 2003; Taylor, 2010).

2.3. Data analysis

We calculated annualized mortality rates using the following equation:

$$m = 1 - (N_{t2}/N_{t1})^{(1/t)}$$

where N_{t1} = number of live trees at initial sampling, N_{t2} = number of trees that survived until the second sampling, and t = number of years between first and second sampling (Sheil et al., 1995).

We tested for differences in the cumulative distribution function of mortality rates among disturbances and vegetation zones based on an F-distribution version of the Wald statistic (Kincaid, 2000) using the cont.cdftest in the package spsurvey (R version 2.13.2). P-values were adjusted (Verhoeven et al., 2005) using the package fdr.tools to account for false discovery rate (Benjamini and Hochberg, 1995) and reduce the potential for Type II errors associated with the large number of comparisons.

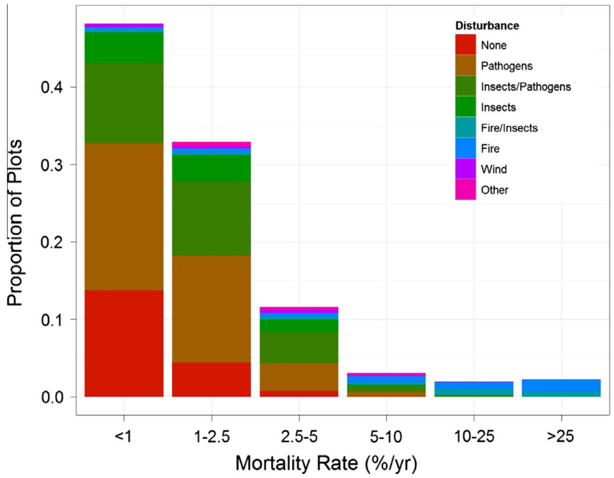

Fig. 3. Distribution of mortality rates by disturbance agent from the mid-1990s to the mid-2000s on USFS lands in Oregon and Washington.

3. Results

Eighty-one percent of the plot-based mortality rates across the region were <2.5%/yr, 11.6% were between 2.5 and <5%/yr, 5.1% were between 5 and 25%/yr, and 2.3% were ⩾25%/yr, and (Fig. 3). Approximately 80% of all the tree mortality (i.e. the total number of trees that died) in wet vegetation zones occurred in plots with pathogens, insects, or no recorded disturbance agent. Patterns in dry vegetation zones were more variable with the proportions of trees dying in plots with evidence of insects and fires ranging from 30 to 60% (Fig. 4).

We found significant differences in the distributions of mortality rates among disturbances (Fig. 5). Rates were lowest in plots where no agent was identified and increased in a distinct order with the occurrence of pathogens, insects, and fire. The co-occurrence of pathogens and insects shifted distributions to higher levels of mortality than with pathogens alone, but did not differ from insects alone. The co-occurrence of insects and fire shifted distributions to higher levels of mortality than with insects alone, but did not differ from fire alone.

We also found significant differences in the distributions of mortality rates among most vegetation zones (Fig. 6). Rates in wet vegetation zones were mostly <2.5%/yr, but distributions in dry vegetation zones were skewed right to higher levels of mortality in plots with evidence of insects and fire. Distributions of mortality rates <2.5%/yr also peaked towards higher levels in wet vegetation zones than in most dry vegetation zones. Rates in undisturbed plots in the subalpine and grand fir/white fir vegetation zones reached similar levels of mortality as those in wet vegetation zones but at lower proportions. Douglas-fir and especially ponderosa pine had the highest proportion of plots with mortality rates <0.5%/yr (Fig. 6). In all vegetation zones, mortality rates in early and mid stages of structural development were primarily <2.5%/yr (Fig. 7). Rates in mature and old-growth stages of structural development reached the highest levels and accounted for most of the rates >2.5%/yr, with less than half of the rates <1%/yr.

4. Discussion

Regional-scale patterns of stand-level tree mortality during the turn of the 21st century reveal tremendous variability in forest dynamics related to natural disturbance and mortality across a diverse region. Our results indicate that, cumulatively, coarse-scale exogenous disturbances have the potential to drive as much

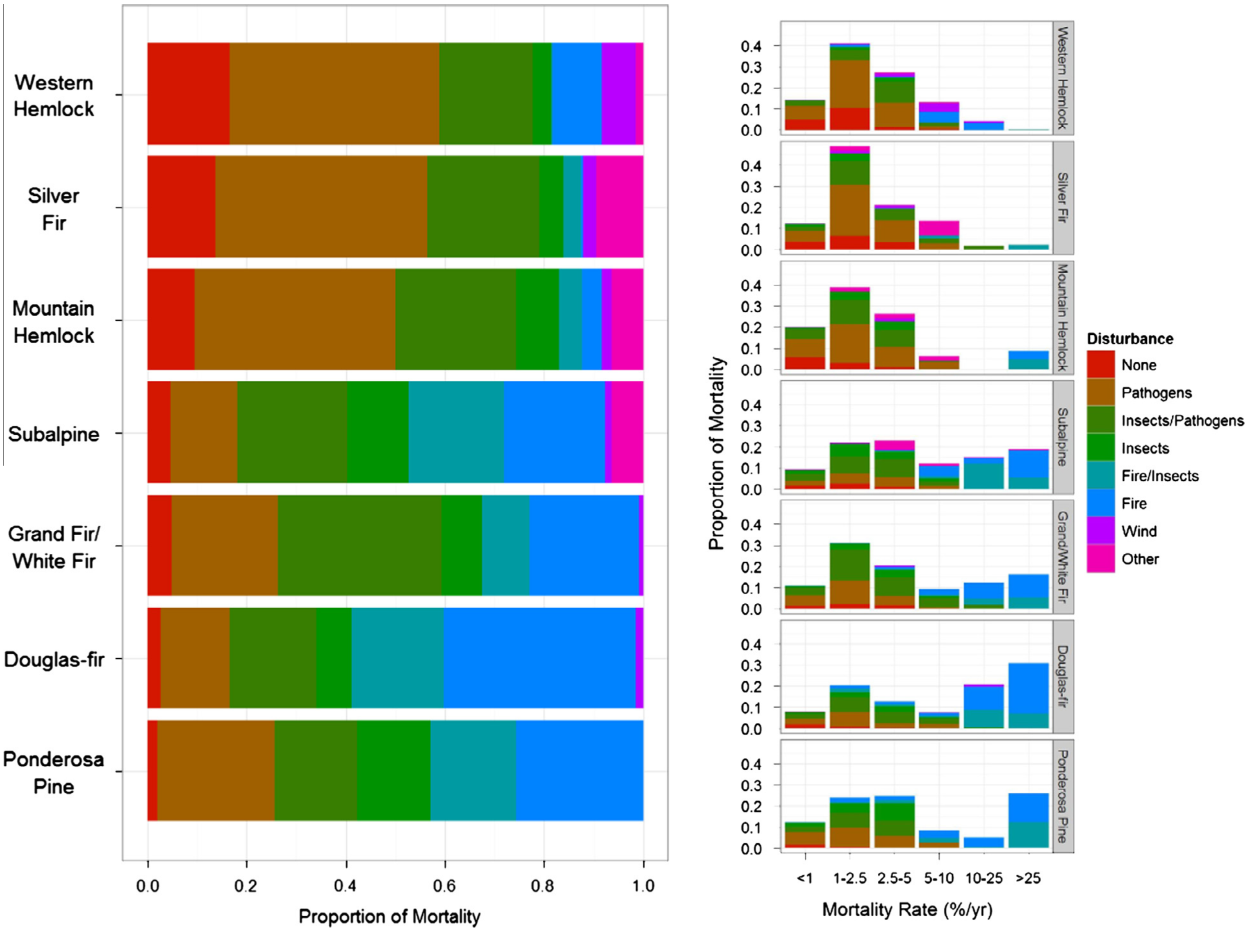

Fig. 4. Patterns of disturbance and tree mortality (total number of trees that died) from the mid-1990s to the mid-2000s in the dominant vegetation zones on USFS lands in Oregon and Washington. The figure on the left depicts the proportion of the total number of trees that died in each vegetation zone. The figure on the right depicts the proportion of the total trees killed at different mortality rates. Other disturbances include floods, landslides, and avalanches.

or more of forest dynamics as fine-scale endogenous processes in some vegetation zones (Spies and Franklin, 1989). The prevalence of intermediate levels of mortality (5–25%/yr) indicative of partial-stand-replacement in exogenous disturbances indicates that most of these disturbances are not stand-replacing and potentially leave considerable live legacies. Conceptualizing endogenous and exogenous disturbances as endpoints of a continuum as opposed to a dichotomy (White and Pickett, 1985) will provide a more comprehensive characterization of the ecological effects of tree mortality and how they vary across a diverse region.

4.1. Disturbance and mortality

Pathogens and insects were pervasive in almost all vegetation zones. Consistent with their primary role in “background” mortality, most mortality rates (>80%) associated with pathogens and insects were within the range (<2.5%/yr) of those found in plots with no evidence of disturbance. Biotic disturbance agents may not result in immediate mortality though their effects may be manifest in decreased growth and vigor (Marias et al., 2014) that initiate the long process of mortality (Manion, 1981) and predispose trees to stem breakage or tip-up later in life (Larson and Franklin, 2010). In some cases, slow rates of spread may require longer periods to manifest mortality related effects, thus the duration of the episode may be at least as important as the mortality rate, particularly when outbreaks are associated with extended drought (Bigler et al., 2007; Carnicer et al., 2011). Biotic agents, particularly insects in dry vegetation zones, did account for mortality rates shifted towards higher levels (1–5%/yr) than in plots with no evidence of disturbance. This is likely related to temperature-driven drought stress that has been linked with increases in background mortality in old-growth forests of the region (van Mantgem et al., 2009) and forest decline which peaked during our study period (Cohen et al., 2016), the warmest decade the region has experienced since the start of the 20th century (Abatzoglou et al., 2014).

Recent studies have expressed concern regarding the occurrence of epidemic insect outbreaks triggered by exogenous stress induced by drought (e.g. Raffa et al., 2008; Carnicer et al., 2011). Despite the occurrence of extreme drought during our study period, mortality rates ⩾5%/yr were rare and most mortality associated with insects was likely limited to localized patches smaller than our 1 ha plots. Ganey and Vojta (2011) found stand-replacing rates (28.5%/yr) associated with insects in a field study with smaller plots (0.09 ha) during drought in the southwestern US. However, rates ⩾10%/yr comprised <1% of all plots with insects, the highest of which occurred as delayed mortality in plots that were subject to fire prior to the initial plot installation. The prevalence of mixed-species stands in the region may increase resistance to epidemic outbreaks since most insects are species-specific. The occurrence of fire following insect outbreaks may also mask higher levels of insect-related mortality, but it seems unlikely given the lack of a positive association between the two within the region and elsewhere (Hart et al., 2015; Meigs et al., 2015). Where the two disturbances did occur together, we found

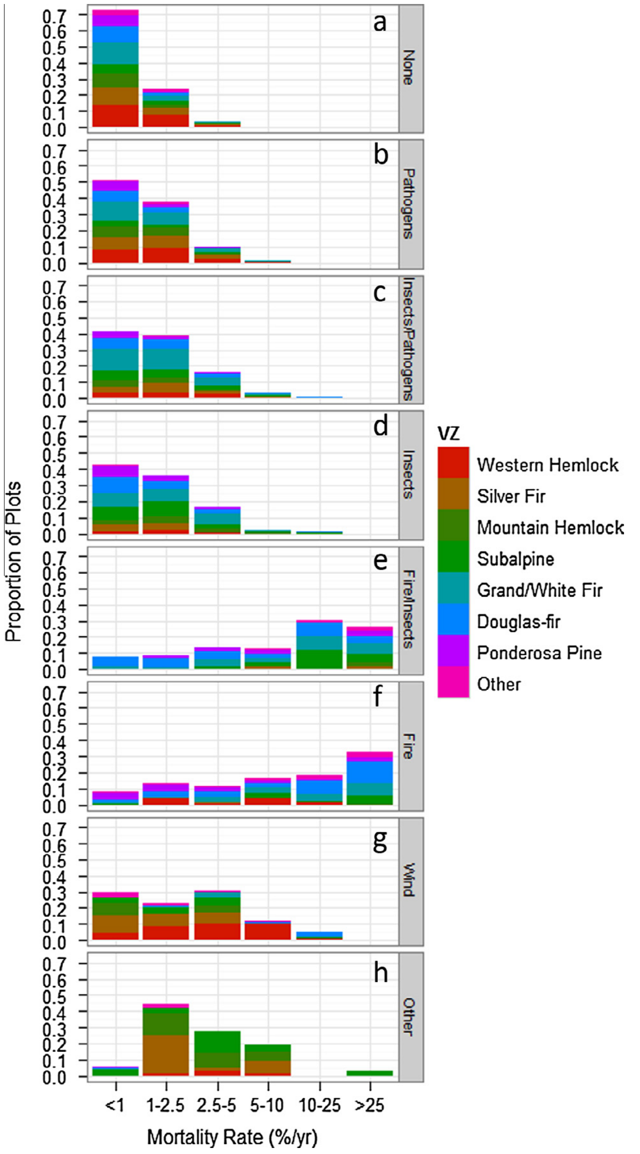

Fig. 5. Distributions of mortality rates for natural disturbance agents on USFS lands in Oregon and Washington from the mid-1990s to the mid-2000s. Disturbances that share the same letter have cumulative empirical distributions that do not differ significantly from each other (p < 0.05) based on a test comparing Wald F-statistics. Other disturbances include floods, landslides, and avalanches.

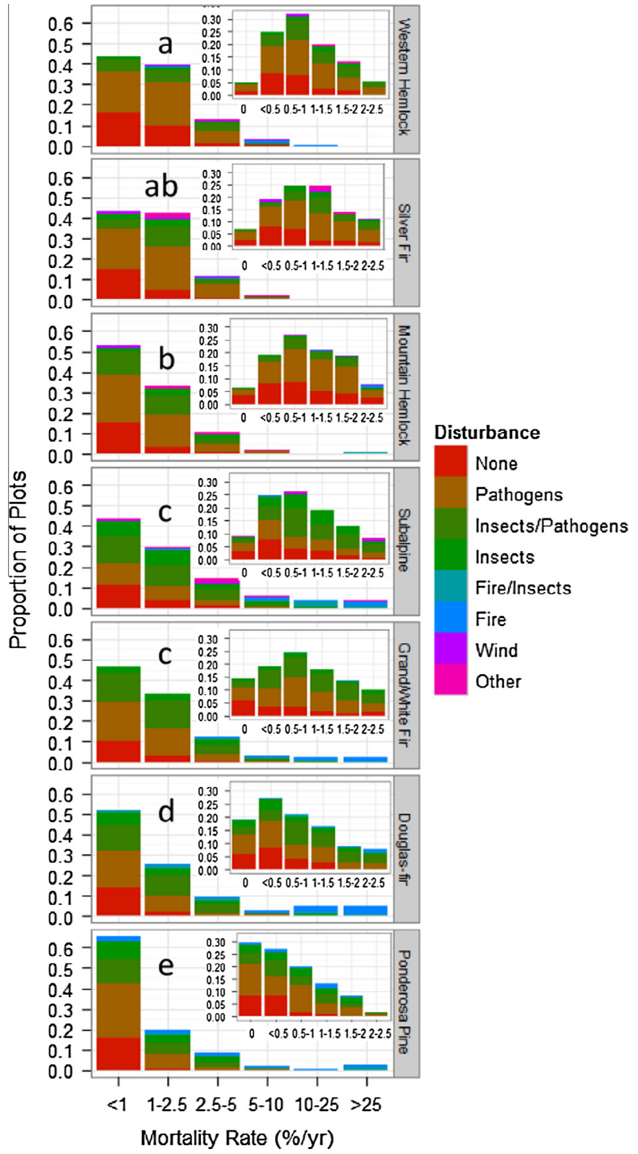

Fig. 6. Distributions of mortality rates in the dominant vegetation zone from the mid-1990s to the mid-2000s on USFS lands in Oregon and Washington. Vegetation zones that share the same letter have cumulative empirical distributions that do not differ significantly from each other (p < 0.05) based on a test comparing Wald F-statistics.

no evidence that the co-occurrence of insects and fire resulted in higher levels of mortality than in fires alone, corroborating a growing number of post-fire studies from around the western United States that pre-fire insect mortality does not necessarily make fires more severe (Simard et al., 2011; Harvey et al., 2013; Agne et al., 2016).

Mortality rates associated with exogenous disturbances were more evenly distributed across higher levels than those associated with endogenous disturbance agents. However, stand-replacing mortality rates (⩾25%/yr) comprised only approximately a third of all rates associated with exogenous disturbance and most rates occurred across intermediate levels of mortality (5–25%/yr). These results indicate a far more common role of exogenous disturbances including floods, wind, and avalanches in altering pathways of structural and successional development (Scott et al., 1985; Greene et al., 1992; Veblen et al., 1994) as opposed to re-initiating dynamics. Stand-replacement by synoptic wind events (Sinton et al., 2000), volcanic eruptions (Turner and Dale, 1998), and landslides are part of the disturbance regimes in the region, but are either too rare to be recorded even in our relatively dense plot-based sampling or occur at intervals longer than our sampling period. Aside from a single plot which fell in an avalanche path, fire was the only natural disturbance that reached stand-replacing mortality rates (⩾25%/yr) and served as the primary source of early seral habitat. During the study period which included several large wildfires (e.g. 200,000 ha Biscuit Fire), stand-replacing mortality affected approximately 2.3% of the study extent which is similar to the 3.8% estimated by Whittier and Gray (2016) using the same data set, but with a different method and plot selection (i.e. different intervals and minimum number of trees).

4.2. Characterizing mortality and dynamics across the region

Most mortality in wet vegetation zones was likely related to fine-scale endogenous processes that operate continuously

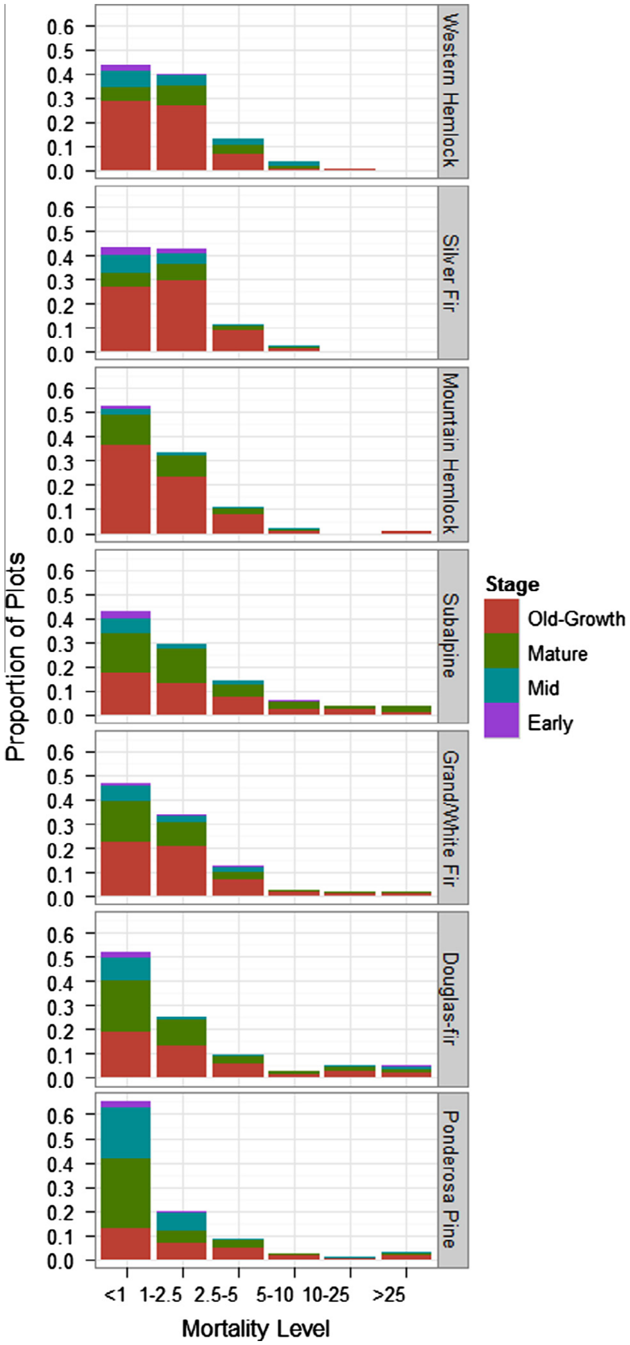

Fig. 7. Histograms of mortality rates by stage of structural development in the major vegetation zone on USFS lands in Oregon and Washington from the mid-1990s to the mid-2000s. Stages of structural development follow those in Reilly and Spies (2015).

throughout stand development (Franklin et al., 2002). Mortality rates in these vegetation zones may be elevated above background levels as a result of individual mortality events from wind or insects (Harmon and Pabst, 2015), but most rates were primarily <2.5%/yr. More complex dynamics associated with chronic wind near the coast (Greene et al., 1992) or long-term decline from pathogens in mountain hemlock (Hansen and Goheen, 2000) do occur, but characterizing the most common forms of mortality as "background" is likely sufficient to describe most dynamics in these vegetation zones. Although infrequent, stand-replacing fire events played a historic role at centennial scales in wet vegetation zones (Weisberg and Swanson, 2003), there is increasing evidence that non-stand-replacing fire played a greater role in southern parts of the western hemlock vegetation zone in central Oregon where most of our sample was located (Agee, 1993; Morrison and Swanson, 1990; Weisberg, 2004; Tepley et al., 2013). Our findings support this and another recent studies that found that recent fires in the western hemlock vegetation zone have been primarily non-stand-replacing (Dunn and Bailey, 2016).

Distributions of mortality rates in dry vegetation zones reveal a more complex set of dynamics with more variability in the role of background mortality and a greater role of partial- and stand-replacing disturbance than in wet vegetation zones. Density-dependent background apparently played a role during our study period in the cooler subalpine and grand fir/white fir vegetation zones where rates in plots without evidence of disturbance reached similar levels as in wet vegetation zones. In contrast, mortality rates in the ponderosa pine and Douglas-fir vegetation zones were extremely low in the absence of disturbance, suggesting a limited role of endogenous processes in the driest vegetation zones aside from pathogens and insects. As opposed to the continuous role of mortality in wet vegetation zones (Franklin et al., 2002), past studies suggest that the role of mortality in some dry forests may be better characterized as an episodic process. Dynamics may fluctuate with periods of little or no mortality followed by elevated mortality during periods of drought such as ours when most mortality is associated with insects or fire (Villalba and Veblen, 1998; Guarin and Taylor, 2005). Most plots that burned in dry vegetation zones (70–80%) experienced non-stand-replacing fire across a wide range of mortality levels. The prevalence of low and moderate severity fires is consistent with some aspects of the historical role of fire in vegetation zones where fire regimes are characterized as low (ponderosa pine) and mixed (grand fir/white fir), but somewhat surprising in the subalpine vegetation zone which is generally characterized as having a stand-replacing fire regime (e.g. Agee, 1993).

4.3. Implications for regional forest change

Our results demonstrate the variability in the magnitude, extent, and drivers of mortality across a regional extent during a period characterized by drought (Abatzoglou et al., 2014), widespread insect activity (Meigs et al., 2015), and wildfire (Littell et al., 2009). Mortality rates in plots in early and mid stages of structural development were relatively low (mostly <2.5%/yr) compared to the 4.4–5%/yr reported in the few demographic studies of mortality we are aware which are limited to wet vegetation zones in the region (Lutz and Halpern, 2006; Larson et al., 2015). Studies from the boreal forest in Canada suggest that younger forests are more susceptible to drought (Peng et al., 2011; Luo and Chen, 2013), but the relatively low rates of mortality in our sample of younger forests compared to published studies indicate the need for a comprehensive analysis and comparison among a range of environments and disturbance histories. Older stages of structural development dominated our sample of Forest Service lands, reflecting the relatively high amounts of older forest that still exist on federal lands in the region (Davis et al., 2015). Mortality rates >1%/yr in over half of the plots in late and old growth stages are consistent with elevated mortality rates associated with cumulative decreases in basal area and density in old-growth forests across the western U.S. during the same time period (van Mantgem et al., 2009).

Ecological change in dry vegetation zones was also driven by partial- and stand-replacing insects and fire. Very large (>1000 ha) patches of high-severity fire (Donato et al., 2009; Cansler and McKenzie, 2014) have the potential for substantial landscape scale change in some parts of the region, but stand-replacing fire affected a relatively small proportion of individual dry vegetation zones (2.1–5.1%). These findings substantiate the observation that structurally diverse, early seral habitats are rare in the region compared to the extent in late and old-growth stages of structural development (Reilly and Spies, 2015) where we observed most fire activity during our study period. Mortality rates (2.5–5%/yr) exceeding even the elevated background levels reported by van Mantgem et al. (2009) and partial-stand-replacing rates (5–25%/yr) were more common than stand-replacing fire and affected from 10–15% and 3.1–7.7% of individual dry vegetation zones, respectively. The ecological effects of mortality at these intermediate levels, however, are the most variable and poorly understood (Frelich and Reich, 1998; Perry et al., 2011). Partial-stand-replacing disturbances with annualized mortality rates from 5% to 25%/yr may kill 25–75% of the trees, but still leave a range of residual live structure and can have a variety of effects including the acceleration of successional change (Abrams and Scott, 1989; Veblen et al., 1994), increasing resistance to future disturbance by insects (Waring and Pitman, 1985) and fire (Agne et al., 2016), and even restoring some aspects of historical structure by decreasing density and increasing the dominance of big trees (Reilly and Spies, 2015).

5. Conclusions

Our results demonstrate the tremendous variability in the magnitude, extent, and drivers of stand-level mortality across a biophysically diverse region during a period characterized by drought (Abatzoglou et al., 2014), widespread insect activity (Meigs et al., 2015), and wildfire (Littell et al., 2009). Elevated mortality rates associated with pathogens and insects in most of the plots in the late and old-growth stages of development corroborate previous findings and indicate the potential for pervasive changes in the older forests that dominate all vegetation zones. Partial- and stand-replacing fire was associated with most mortality in dry vegetation zones, but affected a relatively small proportion of each. These disturbances have likely affected regional biodiversity through the creation of early seral habitat, increased within-stand heterogeneity, and restored of aspects of historical fire regimes, but the ecological effects of intermediate levels of mortality and how they vary by vegetation zone and environment are poorly understood. Our results highlight the need to elucidate the role of disturbance at intermediate levels and recognize endogenous and exogenous disturbances as endpoints of a continuum to more comprehensively characterize regional forest dynamics.

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References

Abatzoglou, J.T., Rupp, D.E., Mote, P.W., 2014. Seasonal climate variability and change in the Pacific Northwest of the United States. J. Climate 27, 2125–2142.

Abrams, M.D., Scott, M.L., 1989. Disturbance-mediated accelerated succession in two Michigan forest types. For. Sci. 35, 42–49.

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, D.C.

Agne, M.C., Woolley, T., Fitzgerald, S., 2016. Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. For. Ecol. Manage. 366, 73–86.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate – a practical and powerful approach to multiple testing. J. R. Stat. Soc. B 57, 289–300.

Bigler, C., Gavin, D.G., Gunning, C., Veblen, T.T., 2007. Drought induced lagged tree mortality in a subalpine forest in the Rocky Mountains. Oikos 116, 1983–1984.

Cansler, C.A., McKenzie, D., 2014. Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. Ecol. Appl. 24, 1037–1056.

Carnicer, J., Col, M., Ninyerola, M., Pons, X., Sanchez, G., Penuelas, J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proc. Natl. Acad. Sci. 108, 1474–1478.

Clark, D.B., Clark, D.A., 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. J. Ecol. 79, 447–457.

Cohen, W.B., Yang, Z., Stehman, S.V., Shroeder, T.A., Bell, D.M., Masek, J.G., Huang, C., Meigs, G.W., 2016. Forest disturbance across the conterminous United States from 1985–2012: the emerging dominance of forest decline. For. Ecol. Manage. 360, 242–252.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.L., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. Bioscience 51, 723–734.

Davis, R.J., Ohmann, J.L., Kennedy, R.E., Cohen, W.B., Gregory, M.J., Yang, Z., Roberts, H.M., Gray, A.N., Spies, T.A., 2015. Northwest Forest Plan-the First 20 Years (1994–2013): Status and Trends of Late-Successional and Old-Growth Forests. PNW GTR-911. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity fire in the Klamath–Siskyou Mountains. Can. J. For. Res. 39, 823–838.

Dunn, C.D., Bailey, J.D., 2016. Tree mortality and structural change following mixed-severity fire in *Psuedotsuga* forests of Oregon's western Cascades, USA. For. Ecol. Manage. 365, 107–118.

Franklin, J.F., Dyrness, C.T., 1973. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.

Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. Bioscience 37, 550–556.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399–423.

Frelich, L.E., Reich, P.B., 1998. Disturbance severity and threshold responses in the boreal forest. Conserv. Ecol. 2, 7.

Ganey, J.L., Vojta, S.C., 2011. Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, USA. For. Ecol. Manage. 261, 162–168.

Greene, S.E., Harcombe, P.A., Harmon, M.E., Spycher, G., 1992. Patterns of growth, mortality, and biomass change in a coastal *Picea-sitchensis – Tsuga heterophylla* forest. J. Veg. Sci. 3, 697–706.

Guarin, A., Taylor, A.H., 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. For. Ecol. Manage. 218, 229–244.

Hansen, E.M., Goheen, E.M., 2000. *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in western North America. Annu. Rev. Phytopathol. 38, 515–539.

Harcombe, P.A., 1987. Tree life tables. Bioscience 37, 557–568.

Harmon, M.E., Pabst, R.J., 2015. Testing predictions of forest succession using long-term measurements: 100 yrs of observations in the Oregon Cascades. J. Veg. Sci. 26, 722–732.

Hart, S.J., Schoennagel, T., Veblen, T.T., Chapman, T.B., 2015. Area burned in the western United States is unaffected by recent pine beetle outbreaks. Proc. Natl. Acad. Sci. 112, 4375–4380.

Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G., 2013. Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. Ecology 94, 2475–2486.

Henderson, J.A., Lesher, R.D., Peter, D.H., Ringo, C.D., 2011. A Landscape Model for Predicting Potential Natural Vegetation of the Olympic Peninsula USA Using Boundary Equations and Newly Developed Environmental Variables Gen. Tech. Rep. PNW-GTR-841. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR (35 p.).

Heyerdahl, E.K., McKenzie, D., Daniels, L.D., Hessl, A.E., Littell, J.S., Mantua, N.J., 2008. Climate drivers of regionally synchronous fires in the inland Northwest (1651–1900). Int. J. Wildland Fire 17, 40–49.

Keane, R.E., Agee, J.K., Fule, P., Keeley, J.E., Key, C., Kitchen, S.G., Miller, R., Schulte, L. A., 2009. Ecological effects of large fires on US landscapes: benefit or catastrophe? Int. J. Wildland Fire 17, 696–712.

Kincaid, T.M., 2000. Testing for differences between cumulative distribution functions from complex environmental sampling surveys. In: 2000 Proceedings of the Section on Statistics and the Environment. American Statistical Association, Alexandria, VA, pp. 39–44.

Larson, A.J., Franklin, J.F., 2010. The tree mortality regime in temperate old-growth coniferous forests: the role of physical damage. Can. J. For. Res. 40, 2091–2103.

Larson, A.J., Lutz, J.A., Donato, D.C., Freund, J.A., Swanson, M.E., HilleRisLambers, J., Sprugel, D.G., Franklin, J.F., 2015. Spatial aspects of tree mortality strongly differ between young and old-growth forests. Ecology 96, 2855–2861.

Littell, J.S., McKenzie, D., Peterson, D.L., Westerling, A.L., 2009. Climate and wildfire burned in the western U.S. ecoprovinces, 1916–2003. Ecol. Appl. 19, 1003–1021.

Logan, J.A., Regniere, J., Powell, J.A., 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. 1, 130–137.

Lugo, A.E., Scatena, F.N., 1996. Background and catastrophic mortality in tropical moist, wet, and rain forests. Biotropica 28, 585–599.

Luo, Y., Chen, H.Y.H., 2013. Observations from old forests underestimate climate change effects on tree mortality. Nat. Commun. 4, 1655. http://dx.doi.org/10.1038/ncomms2681.

Lutz, J.A., Halpern, C.B., 2006. Tree mortality during early forest development: a long-term study of rates, causes, and consequences. Ecol. Monogr. 76, 257–275.

Manion, P.D., 1981. Tree Disease Concepts. Prentice-Hall, Englewood Cliffs, N.J.

Marias, D., Meinzer, F.C., Woodruff, D.R., Shaw, D.C., Voelker, S.L., Brooks, J.R., Lachenbruch, B., Falk, K., McKay, J., 2014. Impacts of dwarf mistletoe on the physiology of host *Tsuga heterophylla* trees as recorded in tree-ring C and O stable isotopes. Tree Physiol. 34, 595–607.

Max, T.A., Schreuder, H.T., Hazard, J.W., Oswald, D.D., Teply, J., Alegria, J., 1996. The Pacific Northwest Region Vegetation and Inventory Monitoring System. USDA Forest Service, Pacific Northwest Research Station, Portland, OR (Research Paper PNW-493).

Meddens, A.J.H., Hicke, J.A., Ferguson, C.A., 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecol. Appl. 22, 1876–1891.

Meigs, G.W., Kennedy, R.E., Gray, A.N., Gregory, M.J., 2015. Spatiotemporal dynamics of recent mountain pine beetle and western spruce budworm out breaks across the Pacific Northwest. For. Ecol. Manage. 339, 71–86.

Morrison, P.H., Swanson, F.J., 1990. Fire History and Pattern in a Cascade Range Landscape. PNW-GTR-254. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Muir, P.S., 1993. Disturbance effects on structure and tree species composition of *Pinus contorta* forests in western Montana. Can. J. For. Res. 23, 1617–1625.

Oliver, C.D., Larson, B.C., 1990. Forest Stand Dynamics. McGraw-Hill, New York, New York, USA.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., Zhou, X., 2011. A drought induced pervasive increase in tree mortality across Canada's boreal forest. Nat. Climate Change 1, 467–471.

Perry, D.A., Hessburg, P.F., Skinner, C.N., Spies, T.A., Stephens, S.L., Taylor, A.H., Franklin, J.F., McComb, B., Riegel, G., 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. For. Ecol. Manage. 262, 703–717.

Pfister, R.D., Arno, S.F., 1980. Classifying forest habitat types based on potential climax vegetation. For. Sci. 26, 52–70.

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

Reilly, M.J., Spies, T.A., 2015. Regional variation in stand structure and development in forests of Oregon, Washington, and inland Northern California. Ecosphere 6, 192. http://dx.doi.org/10.1890/ES14-00469.1.

Scott, M.L., Sharitz, R.R., Lee, L.C., 1985. Disturbance in a cypress-tupelo wetland: an interaction between thermal loading and hydrology. Wetlands 5, 53–68.

Seidl, R., Schelhaas, M.-J., Rammer, W., Vererk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nat. Climate Change 4, 806–810.

Shaw, J.D., Steed, B.E., Deblander, L.T., 2005. Forest inventory and analysis (FIA) annual inventory answers the question: what is happening to pinyon-juniper woodlands? J. Forestry 103, 280–285.

Sheil, D., Burslem, D.F.R.P., Alder, D., 1995. The interpretation and misinterpretation of mortality-rate measures. J. Ecol. 83, 331–333.

Simard, M., Romme, W.H., Griffin, J.M., Turner, M.G., 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol. Monogr. 81, 3–24.

Sinton, D.S., Jones, J.A., Ohmann, J.L., Swanson, F.J., 2000. Windthrow disturbance, forest composition, and structure in the Bull Run Basin, Oregon. Ecology 81, 2539–2556.

Spies, T.A., Franklin, J.F., 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology 70, 543–545.

Taylor, A.H., Skinner, C.N., 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecol. Appl. 13, 704–719.

Taylor, A.H., 2010. Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades, USA. J. Veg. Sci. 21, 561–572.

Tepley, A.J., Swanson, F.J., Spies, T.A., 2013. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest. Ecology 94, 1729–1743.

Turner, M.G., Romme, W.H., Gardner, R.H., O'Neil, R.V., Kratz, T.L., 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. Landscape Ecol. 8, 213–227.

Turner, M.G., Dale, V.H., 1998. Comparing large infrequent disturbances: what have we learned? Ecosystems 1, 493–496.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524.

Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M., Villalba, R., 1994. Disturbance interactions in a Rocky Mountain subalpine forest. J. Ecol. 82, 125–135.

Verhoeven, K.J.F., Simonsen, K.L., McIntyre, L.M., 2005. Implementing false discovery rate control: increasing your power. Oikos 108, 643–647.

Villalba, R., Veblen, T.T., 1998. Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. Ecology 79, 2624–2640.

Waring, R.H., Pitman, G.B., 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. Ecology 66, 889–897.

Weisberg, P.J., 2004. Importance of non-stand-replacing fire for development of forest structure in the Pacific Northwest USA. Forest Sci. 50, 245–258.

Weisberg, P.J., Swanson, F.J., 2003. Regional synchroneity in fire regimes of western Oregon and Washington, USA. For. Ecol. Manage. 172, 17–28.

White, P.S., 1979. Pattern, process, and natural disturbance in vegetation. Botanical Rev. 45, 229–299.

White, P.S., Pickett, S.T.A., 1985. Natural disturbances and patch dynamics: an introduction. In: Pickett, S.T.A., White, P.S. (Eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic, New York, pp. 3–13.

Whittier, T.R., Gray, A.N., 2016. Tree mortality based fire severity classifications for forest inventories: a Pacific Northwest national forests example. For. Ecol. Manage. 359, 199–209.

Williams, A.P., Allen, C.D., Millar, C.I., Swetnam, T.W., Michaelsen, J., Still, C.J., Leavitt, S.W., 2010. Forest response to increasing aridity and warmth in the southwestern United States. Proc. Natl. Acad. Sci. 107, 21289–21294.