



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 ($\geq 25\%/yr$) 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.

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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 (*Pseudotsuga*

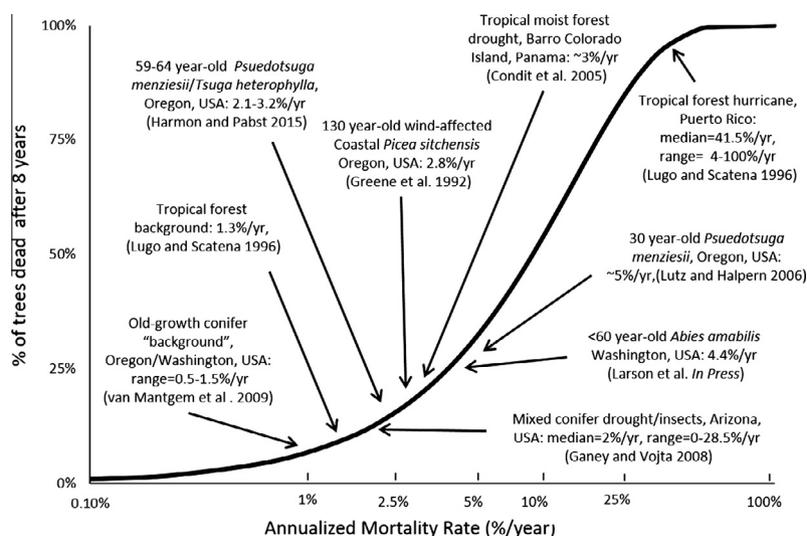


Fig. 1. Cumulative percent of trees dying after eight years at corresponding stand mortality rates along with published mortality rates from selected studies. Demographic studies of tree mortality annualize mortality rates as study intervals often vary. Thus, a mortality rate of 10%/yr over an eight 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.)

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