Do denser forests have greater risk of tree mortality: A remote sensing analysis of density-dependent forest mortality

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ABSTRACT

In forests of the western United States, high levels of forest stocking attributed to fire exclusion and settlement-era logging practices have coincided with periods of extensive forest mortality associated with extreme drought and forest pest outbreaks. This has led to the widespread but largely untested generalization that increased stand density causes increased levels of forest mortality, even for uneven-aged, multi-species, mature stands that are not actively undergoing self-thinning. We used archival Landsat imagery to examine: (1) variations in forest mortality among forest types and climate periods from 1985 to 2010 in the mixed conifer forest of the Lake Tahoe Basin, (2) relationships between stand density and mortality in the subsequent year, and (3) the influence of environmental variables on forest mortality. We found that positive density dependent mortality, where increased stand density is associated with increased probability of mortality, is associated more with lower elevation forests and drier climate periods. In mid- to upper-elevation forests, increased density was more often associated with decreased probability of mortality, especially during wetter periods. Results showed highest tree mortality during a drought in the beginning of our 25-year time series, but not in a subsequent drought period of similar severity. Our study also found increased risk of tree mortality on north-facing slopes across all forests and all climate periods, even when stand density was controlled for. There is a nuanced relationship between stocking level, forest mortality and drought effects, suggesting that no single density-reduction forest management strategy will increase forest resilience under all climate periods and in all forest types.

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1. Introduction

Widespread and synchronous outbreaks of forest mortality since the mid-20th century have drastically altered millions of hectares of forestlands from Mexico to Alaska (Allen et al., 2010; Anderegg et al., 2012; Bentz, 2009), with mortality rates doubling every 17–29 years in some areas (van Mantgem et al., 2009). Many forest types have experienced recent large-scale tree mortality events, including whitebark pine (*Pinus albicaulis*) in the Greater Yellowstone Ecosystem (Logan et al., 2010) and the Sierra Nevada (Millar et al., 2012); mixed conifer stands of the Sierra Nevada (Ferrell et al., 1994; Guarín and Taylor, 2005; Millar et al., 2012; van Mantgem et al., 2009); ponderosa pine (*Pinus ponderosa*), mixed conifer, and pinyon-juniper woodlands of the Southwestern US (Breshears et al., 2005; Floyd et al., 2009; Ganey and Vojta,

2011; Meddens et al., 2015); subalpine and middle-elevation forests of Utah and Colorado (DeRose and Long, 2007,2012; Hebertson and Jenkins, 2008), lodgepole pine forests of British Columbia, Canada (Aukema et al., 2006); spruce forests of Alaska (Berg et al., 2006), and temperate coniferous forests of Europe (Allen et al., 2010; Dobbertin et al., 2007). Though periods of high forest mortality have occurred at various times in the past and may be considered an intrinsic component of natural variability (DeRose and Long, 2007), many recent studies have emphasized the link between drought and forest mortality (Allen et al., 2010; Anderegg et al., 2012; Breshears et al., 2005; Dobbertin et al., 2007; Floyd et al., 2009). While a strong association between drought and mortality is expected, not all drought events are associated with forest health problems. Factors contributing to variations in mortality levels over multiple dry and wet periods for the same forest landscape are not well understood.

Forest mortality can be either patchy or widespread, occurring at chronic background levels with small groups of trees affected, or at outbreak levels with widespread tree die-off across much of

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the landscape. Causes of forest mortality and the conditions that give rise to outbreaks of widespread mortality are complex and hard to predict (Bentz et al., 2010; Berg et al., 2006; Dukes et al., 2009). Forest mortality is influenced by both bottom-up drivers, such as the physical environment of the stand, individual tree characteristics and forest structure, and top-down drivers, such as climate and biotic disturbances mediated by a variety of insects and pathogens (Allen et al., 2010; Millar et al., 2012; Pedersen, 1998; Raffa et al., 2008; van Mantgem et al., 2009). It is expected that bottom-up and top-down drivers interact, although the precise nature of the interaction is not well known for many forest types. In the western United States, much forest mortality is directly caused by native bark beetles (Coleoptera: Scolytinae), although more proximal exogenous factors such as drought, and endogenous factors such as stand density and environmental setting are also important (Allen et al., 2010; Raffa et al., 2008).

In coniferous forests, mortality is mediated by a diverse array of host-specific pests and pathogens that interact with edaphic and climatic factors, as well as individual tree characteristics, to suppress growth or cause tree mortality (Castello et al., 1995). In Western forests, a majority of mortality is mediated by bark beetles (Dendroctonus, Ips, Scolytus) which attack during the late Spring to early Fall and, in the case of a successful attack, excavate egg galleries in the inner bark from which new beetles emerge in the next Spring (Table 1, Christiansen et al., 1987; Ferrell, 1996). Successful attack by bark beetle in one tree in a crowded stand can increase probability of attack to proximate conspecifics, due to increased numbers of bark beetles in the stand as well as proximity to infected trees (Christiansen et al., 1987; Das et al., 2008; Raffa and Berryman, 1983). Proximate and touching canopies and tree root systems can facilitate the spread of damage agents such as dwarf mistletoe (Arceuthobium spp.) and root rots which decrease photosynthetic capacity (Aukema et al., 2010; Cruickshank et al., 1997; Maloney and Rizzo, 2002). Infection by these damage agents may further weaken trees, predisposing them to mortality due to bark beetle attack (Ferrell, 1996; Kenaley et al., 2008, but see Maloney and Rizzo, 2002). Increased forest homogeneity, decreased structural complexity, decreased species diversity, and increased stand density resulting from fire exclusion can lead to more extensive mortality by increasing supply and continuity of food resources for host-specific bark beetles (Moritz et al., 2010; Perry et al., 2011).

In coniferous forests of the western U.S. and Europe, increased stand density and inter-tree competition resulting from fire exclusion and post-settlement timber harvesting practices are widely hypothesized to increase forest-wide mortality levels (Dobbertin et al., 2007; Guarín and Taylor, 2005; Millar et al., 2012; Maloney et al., 2011). Positive density-dependent mortality (positive DDM) where increases in stand density are associated with increased probability of mortality and its inverse, negative DDM, where decreases in density are associated with increased probability of mortality, both operate in forest ecosystems (Das et al., 2011). While less well documented than positive DDM, negative DDM has been demonstrated in environmentally stressful sites where facilitation effects can be important for survivorship and growth of both seedlings and mature trees, including arid juniper woodlands (Bowker et al., 2012) and high-elevation Abies lasiocarpa in subalpine forests of the Rocky Mountains (Callaway, 1998). Although DDM plays a critical role in early stand development through self-thinning (Reineke, 1933; Yoda et al., 1963), its role in structurally mature forests is less well understood (Das et al., 2011; Peet and Christensen, 1987; Vygodskaya et al., 2002).

One hypothesized mechanism for the link between mortality and density is based on optimal defense theory in which sustained inter-tree competition for shared critical resources limits the ability of trees to generate the energy-intensive chemical and physical structures necessary to survive pest and pathogen attacks (Herms and Mattson, 1992; Raffa and Berryman, 1983; Stamp, 2003). Positive DDM has been supported by some studies of individual tree mortality in which trees in dense stands showed slower growth and decreased water use efficiency, limiting adaptive response to drought conditions (Linares et al., 2009, 2010). Increased stand density can also mediate faster and more extensive spread of pests and pathogens within the stand and the surrounding forest (Peet and Christensen, 1987; Das et al., 2008). Proximate and touching canopies and tree root systems can facilitate the spread of damage agents such as dwarf mistletoe (Arceuthobium spp.) and root rots which decrease photosynthetic capacity (Aukema et al., 2010; Cruickshank et al., 1997; Maloney and Rizzo, 2002). Increased forest homogeneity stemming from decreased structural complexity, decreased species diversity, and increased stand density resulting from fire exclusion can lead to more extensive mortality by increasing supply and continuity of food resources for host-specific bark beetles (Moritz et al., 2010; Perry et al., 2011).

Recent studies of epidemic forest mortality events have not found stand density to be a significant contributor to tree death and instead, have attributed forest declines to the effects of top-down drivers such as moisture stress and drought, and associated spread and proliferation of bark beetle populations (Ganey and Vojta, 2011; Lines et al., 2010; Sánchez-Martínez and Wagner, 2002; van Mantgem and Stephenson, 2007). During episodic forest mortality events, the role of site environment, spatial proximity and landscape configuration can become more important than stand characteristics for predicting mortality patterns (MacQuarrie and Cooke, 2011; Powers et al., 1999; Simard et al., 2012). Differences in the importance of tree vigor and spatial aggregation may help explain why hazard ratings based on stand characteristics have little predictive power when applied to landscapes (Logan et al., 1998; Nelson et al., 2007). A comprehensive understanding of the role of density dependence during both epidemic and non-epidemic ("background") mortality periods remains elusive (Stamp, 2003).

Increases in forest mortality rates, projected climatic changes, and concerns about forest health and wildfire severity have led forest management agencies throughout the western United States to implement extensive forest density reductions. The objectives of such density reduction treatments are to mitigate fire risk and restore forest health (Fettig et al., 2007). Although density reduction treatments have demonstrated effectiveness in reducing fire intensity during subsequent wildfires (Graham et al., 1999; Safford et al., 2009), the effectiveness of such treatments for improving long-term forest health is not well demonstrated (Bradley and Tueller, 2001; Fettig et al., 2007, 2008, 2012; Schwilk et al., 2006 but see Giuggiola et al., 2013).

Our overall objective was to quantify the interactive effects of forest density, climate, and site environment for influencing forest mortality levels across several distinct forest types. We used remote sensing analysis of 25 years of Landsat TM archival imagery for the Lake Tahoe Basin to quantify: (1) forest mortality levels, (2) density-dependent mortality, and (3) how density dependence in forest mortality varied by forest type and climate period. We hypothesized that positive density-dependent mortality associated with high stocking levels is more important for lower-elevation forests, because that is where trees experience the greatest competition for water and nutrients. Additionally, we hypothesized that density-dependent mortality is weakest during periods of extreme drought when damage agents such as bark beetle populations become more aggregated, because during such periods the role of spatial proximity and landscape configuration can become more important than stand characteristics (Holdenrieder et al., 2004; Logan et al., 1998; MacQuarrie and Cooke, 2011).