Forest Ecology and Management 366 (2016) 184–192

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Forest composition change after a mountain pine beetle outbreak, Rocky Mountain National Park, CO, USA

Carlyn Perovich *, Jason S. Sibold

Department of Anthropology and Graduate Degree Program in Ecology, Campus Delivery 1787, Colorado State University, Fort Collins, CO 80523, USA

ARTICLE INFO

Article history:
Received 6 November 2015
Received in revised form 4 February 2016
Accepted 4 February 2016
Available online 18 February 2016

Keywords:
Disturbance interactions
Forest change
Mountain pine beetle
Pinus contorta
Rocky Mountains

ABSTRACT

Recent severe and extensive mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreaks have created novel conditions in Southern Rocky Mountain lodgepole pine forests which historically had disturbance regimes dominated by extensive, stand-replacing fires. The goal of this study is to investigate patterns of and potential mechanisms in post-outbreak forest change in order to better understand the ecological legacy of the recent outbreak in the context of its implications for resilience to future disturbances and adaptation to climate change. To this end, we collected field data on forest structure and species composition in 2012 in lodgepole pine dominant forests in Rocky Mountain National Park. We then used a combination of modeling and statistical methods to identify possible mechanisms in post-outbreak forest conditions and evaluate the effect of the MPB outbreak on forest heterogeneity. We found that the outbreak initiated a shift in forest structure from single-cohort lodgepole pine stands to stands with greater diversity in age classes and species composition. This increase in landscape asynchrony may increase resiliency to future disturbances. However, this heterogeneity is a result of more spruce and fir on the landscape, species which are less adapted to projected future climate conditions. Our results indicate that disturbances do not necessarily increase the rate at which vegetation adapts to a changing climate, and that it is essential to consider disturbance type and available seed sources when predicting future forest conditions.

1. Introduction

Disturbance is a key process shaping ecological systems, and as the global climate changes, climate-mediated disturbance regimes are changing rapidly and may become profoundly different over the next century (Turner, 2010). Given projections of increased rates of disturbance in a warming world (Dale et al., 2001), forest systems will be exposed to more disturbance events. Moreover, because disturbances often provide opportunities for new seedling establishment, they may assist landscape adaptation to climate change by facilitating migration (Overpeck et al., 1990). Increased rates of disturbance will also increase the likelihood that disturbances will interact with one another, through multiple events of the same type (i.e. more frequent fire), or events of different types (a beetle outbreak followed by a fire). Disturbance interactions can produce synergistic effects (Paine et al., 1998), which are contingent on the order and timing of the disturbances in question (Davies et al., 2009; Miao et al., 2009). Disturbances and their interactions also affect the type and amount of post-disturbance regeneration (Sibold et al., 2007; Kulakowski et al., 2013; Harvey et al., 2014a,b; Edwards et al., 2015) and could lead to ecological surprises (Paine et al., 1998). The goal of this study is to investigate patterns of and potential mechanisms in post-outbreak forest change in order to better understand the ecological legacy of the recent outbreak in the context of its implications for resilience to future disturbances and adaptation to climate change.

Interactions among disturbances including fires, bark beetle outbreaks, avalanches, and wind blowdowns play a central role in shaping patterns of landscape conditions in the subalpine forest zone of the Southern Rocky Mountains. Disturbances leave ecological legacies through their influences on stand age, structure, and species composition, which in turn can affect the likelihood, extent, and severity of future disturbances. For example, fire history affects the likelihood and severity of subsequent bark beetle outbreaks (Veblen et al., 1994; Bebi et al., 2003), the severity of subsequent blowdown events (Kulakowski and Veblen, 2002), and the likelihood (Bigler et al., 2005) and extent (Kulakowski and Veblen, 2007) of subsequent fires, with more recently burned stands less susceptible to all three disturbances. Pre-fire disturbance history, in turn, can influence fire likelihood and severity. Pre-fire bark beetle outbreaks may affect fire likelihood, with one

* Corresponding author.
E-mail address: carlynperovich@gmail.com (C. Perovich).

http://dx.doi.org/10.1016/j.foreco.2016.02.010
0378-1127/

study finding a slight increase in likelihood in post-outbreak forests (Bigler et al., 2005), although others (Bebi et al., 2003; Hart et al., 2015; Meigs et al., 2015) found no relationship. Fire severity may be increased by prior severe blowdowns (Kulakowski and Veblen, 2007) and can be linked to pre-fire beetle outbreak severity, though this relationship is dependent on outbreak stage and weather conditions (Harvey et al., 2014a,b).

Disturbance types and interactions can also affect post-disturbance regeneration. Sibold et al. (2007) found that lodgepole pine establishment was facilitated by higher-severity disturbances (>80% mortality) that occurred in younger (<150 years) post-fire stands, while subalpine fir establishment was facilitated by lower-severity disturbances that occurred in older post-fire (>150 years) stands. Similarly, in MPB with subsequent fire scenarios, areas with MPB and high fire severity had the densest lodgepole regeneration (Harvey et al., 2014a,b; Edwards et al., 2015), while areas with MPB and no fire favored subalpine fir regeneration (Edwards et al., 2015). Kulakowski et al. (2013) found increased aspen regeneration in stands affected by blowdown then fire compared to stands only affected by fire, and Buma and Wessman (2011) found that the severity of a pre-fire blowdown event affected the quantity of post-fire regeneration.

The recent mountain pine beetle outbreak in the Southern Rockies is unprecedented in recorded history in its severity, extent, and duration (Raffa et al., 2008) and has extensively reshaped forested landscapes in the region. Mountain pine beetles have historically existed at both endemic and eruptive levels, but MPB outbreaks in the past 20 years have affected over 25 million hectares of forest across the Western United States and Canada (Meddens et al., 2012), expanding into areas that have rarely or never been impacted by bark beetles in the past (Logan et al., 2003). The exceptional nature of the recent outbreaks is most likely due to the combination of a prolonged period of abnormally warm temperatures (Klutsch et al., 2009), and a homogenous landscape of large lodgepole pine, an ecological legacy of extensive subalpine fires in the late 1800 s (Kipfmueller and Baker, 2000; Buechling and Baker, 2004; Sibold et al., 2006).

Historically, the lodgepole pine forest type throughout the southern Rocky Mountains has been most obviously shaped by a disturbance regime of infrequent high-severity, stand-replacing fires (Kipfmueller and Baker, 2000; Buechling and Baker, 2004; Sibold et al., 2006), which initiated single-cohort stands of lodgepole pine (Sibold et al., 2007; Axelson et al., 2009). As such, our understanding of the ecological legacy of this MPB outbreak is limited. Previous MPB outbreaks in the United States and British Columbia have increased the relative abundance of non-host species (Sibold et al., 2007; Astrup et al., 2008; Nigh et al., 2008; Amoroso et al., 2013; Alfaro et al., 2015); and prior research on the recent MPB outbreak indicates similar species shifts are occurring in our study area (Diskin et al., 2011; Nelson et al., 2014) and elsewhere (Kayes and Tinker, 2012; Briggs et al., 2015).

While the occurrence of post-outbreak changes in species composition is well documented, there remains a lack of quantitative understanding of what mechanisms may be involved and how these shifts might play out across the landscape. Moreover, prior research in our study area (Diskin et al., 2011; Nelson et al., 2014) sampled as the MPB outbreak was still ongoing, assumed that all seedlings preceded the outbreak, and focused largely on advanced regeneration as the primary mechanism for forest regeneration. Advanced regeneration may be a more important factor in forest regeneration in terms of silvicultural needs, as larger remaining trees will enhance the recovery of basal area and the ability to meet stocking requirements. From an ecological perspective, however, composition of newly established seedlings will also be integral in defining the long-term ecological legacy of the outbreak (*sensu* Amoroso et al., 2013).

To elucidate the ecological consequences of the recent MPB outbreak in the Southern Rockies and improve our understanding of post-outbreak forest change, we quantified post-MPB forest composition and size structure in the field and used Bayesian regression analysis to further investigate post-outbreak forest change. Our analysis focuses on the following questions:

1. How has the forest structure and composition changed as a result of the recent MPB outbreak?
2. What are the patterns of and potential mechanisms in this forest change?

2. Methods

2.1. Study area

We addressed these questions in the lodgepole pine forest type of Rocky Mountain National Park (RMNP). The park (located at 40.33°N, 105.71°W) covers 108,000 ha and spans elevations from 2240 to 4350 m on both sides of the Continental Divide in the Northern Colorado Front Range. Our study was confined to the west side of the divide, which was severely affected by the recent MPB outbreak. The nearest weather station to the study area in Grand Lake, CO records an average yearly minimum temperature of −17.5 °C in January and average yearly maximum temperature of 24.6 °C in July. Average annual precipitation is 48.26 cm, with an average of 21.68 cm falling as snow (Western Regional Climate Center, 2012).

The recent mountain pine beetle outbreak first appeared in western RMNP in 2002, was widespread on the landscape from 2005 to 2007, and began to subside in 2008 after exhausting most suitable host trees (USDA Forest Service, 2012; Diskin et al., 2011). Most of the pre-outbreak forest landscape regenerated following widespread fires in the second half of the nineteenth century, although some stands date back to the 1600 s and 1700 s. These large, high-severity fires created a fairly homogenous forest characterized by expansive single-cohort patches of predominantly lodgepole pine at elevations from 2500 to 3300 m. Higher-elevation and mesic sites at lower elevations, such as north-facing slopes, are dominated by Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) (Sibold et al., 2006, 2007).

2.2. Field methods

We randomly selected sampling sites stratified by elevation and aspect from a digital elevation model (Gesch et al., 2002), time since fire based on age structure and fire scars (Sibold et al., 2006), and distance to spruce-fir dominant forest (Sallas et al., 2005). At each site we quantified forest species composition and size structure in two 20 × 20 m plots, which were separated by 100 m at a random azimuth. Because plots at the same site often exhibited very different species composition and size structures, we treated each plot as an independent sample in analysis.

We sampled 218 plots at 109 sites on the west side of Rocky Mountain National Park in the summer of 2012 (Fig. 1). In each plot all trees were assessed for species, DBH, and status (live, dying, recently dead, long dead) and species, height, and status (live or dead) were recorded for seedlings (stems <1.37 m in height). Recently dead (<10 years before present) and long dead trees (>10 years before present) were differentiated based on the amount of fine branches and needles that remained on the tree and how intact the bark was (Keen, 1955). In order to delineate pre- and post-outbreak seedling establishment, we estimated seedling age based on terminal bud scar counts (Urza and Sibold, 2013). Seedlings with five or fewer distinguishable bud scars were assigned an age equal to the number of scars. We found that most seedlings did not have more than six clear bud scars, so all