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Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire

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ABSTRACT

The recent mountain pine beetle (MPB) outbreak across western North America's interior lodgepole pine forests has altered the landscape such that the majority of wildfires in the region will now burn through MPB-affected stands. Study of plant community response to these combined disturbances is critical for our understanding and management of these pine forests. Based on data collected from an experimental burn project in central interior British Columbia, Canada, we investigate variation in understory plant communities along a gradient of disturbance that includes MPB-only and red-phase MPB + fire across three levels of fire severity. We compare communities pre-fire and five years post-fire using three hypotheses that predict community response to disturbance: the light hypothesis, the divergence-convergence hypothesis, and the fire severity begets pine hypothesis.

Comparisons of pine and fir tree seedling tallies suggest a divergence in composition along the disturbance severity gradient. Pine seedlings were mostly absent from the unburned treatment but dominated the burned treatments with densities increasing at higher severities. For the non-tree understory community, canopy-opening associated with both unburned and with low through moderate-high severity burning results in a convergence of general plant community structure demonstrated by rank-abundance curves, but divergent community membership associated with fire severity and fire-adaptive traits. Communities in the unburned treatment saw a release due to canopy opening that supported increases in the dominant shrubs and understory fir seedlings. In the burned treatments, shrubs also increased in dominance and community membership was determined by fire-adaptive traits with fire-adapted species being most abundant in the highest severity fire treatments. Overall, the communities appear to be resilient to the combined effects of MPB (red-phase) and low to moderate-high severity burning, but further research is required in the grey-phase of beetle-kill to broaden our understanding of the landscape legacy of this recent insect outbreak.

1. Introduction

Western North America's recent mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreak has altered the central interior lodgepole pine (*Pinus contorta* var. *latifolia*) forests of British Columbia (BC) such that the majority of wildfires there will now burn through MPB-affected stands. A history of landscape burning in the BC interior (Wong et al., 2003) suggests post-fire seral stages of lodgepole-associated plant communities should be well adapted for recovery after fire, however recovery from the combined effects of MPB followed by fire is a process about which we know very little. Research to date has largely focused on tree regeneration after MPB (e.g. Collins et al., 2010, 2011; Hawkins et al., 2012; McIntosh and Macdonald, 2013; Vyse et al., 2009), and after combined MPB and fire (e.g. Harvey et al., 2014a,b), with minimal study of broader understory plant community response to either of these disturbance scenarios (Dhar and Hawkins, 2011; but see Stone and Wolfe, 1996). The initial trajectory of the understory layer after disturbance can influence ecosystem functioning, future community composition, and overstory canopy development (Gilliam, 2007; Nilsson and Wardle, 2005; Royo and Carson, 2006). Accordingly, a focused study to examine understory plant community response to MPB and subsequent overlap with fire is critical to

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our understanding of successional dynamics in these pine forests and will provide information valuable to forest ecosystem management and conservation of biodiversity.

The recent MPB outbreak has resulted in broad and on-going changes to the composition and configuration of affected forest stands. Estimates for BC indicate MPB has affected more than 18 million hectares of lodgepole pine forest as of 2012 (BC MFLNRO, 2012). The initial phase of MPB outbreak is called the green-attack-phase, where trees have been attacked but retain green needles (<1 year after infestation; Harvey et al., 2014a). This is followed by the red-phase, where needles turn from green to red and remain on the dead and dying trees for roughly one to three years. Once these red needles fall to the ground, trees enter the grey-phase. Eventually these dead, grey-phase snags will fall resulting in old-phase forests (Hicke et al., 2012). Observed effects on forest stands from the death of pine trees include increased light reaching the forest floor due to loss of needles from overstory trees, and altered soil moisture and substrate conditions for understory plants and seeds (Dhar and Hawkins, 2011). The plant community effects of canopy opening due to MPB can be broadly referred to as a 'release' of the understory. Stone and Wolfe (1996) for example, found that understory biomass increased exponentially in response to initial canopy mortality from MPB, with greatest species richness at moderate disturbance severities. Stands dominated by lodgepole pine but containing subalpine fir (*Abies lasiocarpa*) in the subcanopy or understory show a high proportion of fir post-outbreak (Astrup et al., 2008; Nigh et al., 2008). This shift in dominance from pine to fir is likely due to limited activation of the serotinous seed bank of lodgepole pine and canopy-opening that promotes enhanced growth, or release, of shade tolerant understory fir saplings (Griesbauer and Green, 2006), notionally following the tolerance model of Connell and Slatyer (1977).

Fire plays an important role in the dynamics of lodgepole pine dominated forests (Agee, 1993). In central BC, stand replacing fires influence plant community composition by filtering for traits adapted to local and landscape disturbance characteristics. Rowe (1983) developed a broad classification system based on plant response to disturbance and though the groupings are not based exclusively on fire, they provide a broadly accepted classification, hereafter referred to as fire-adaptive traits. Within Rowe's (1983) classification *Invaders* are defined as highly dispersive pioneers, including short-lived perennials. *Endurers* are species able to resprout either from above- or below-ground structures when top-killed by fire. The capacity to endure varies with fire severity and soil heating, but plants with the endurer strategy, particularly woody shrubs, dominate understory communities in central BC. *Avoiders* are late successional, shade-tolerant species that have no obvious adaptation to fire and tend to be absent from early seral, post-fire communities. *Evaders* are species with long-lived propagules stored in the soil or canopy seed bank and can often take advantage of post-fire conditions. Lodgepole pine is considered an evader, producing serotinous cones that remain sealed with resin until sufficiently heated. Once opened (usually by fire), seeds are released onto the newly exposed mineral soil to propagate a new cohort.

MPB and fire have occurred together in western pine forests with idiosyncratic overlap, but the extent of the recent MPB outbreak is such that overlap of MPB and fire disturbances will become common. We define short-interval disturbance wherein the second disturbance, in this case fire, occurs before the forest has recovered from the initial disturbance, in this case MPB. An extension of a short-interval disturbance is a compound disturbance, *sensu* Paine et al. (1998), wherein the short disturbance interval produces a different ecological effect from what would be expected after the second disturbance alone, sometimes referred to as a multiplicative effect (Paine et al., 1998). Short-interval disturbances can also be linked, where the occurrence or severity of the first event affects that of the second (Simard et al., 2011), however short-interval disturbance can produce compound effects even if the disturbances are not linked (Harvey et al., 2013). A linked disturbance could occur if the MPB outbreak generates changes in the fuel structure of the forest that then alters fire behaviour or severity.

Even without a linked change in fire behaviour, the short-interval MPB + fire disturbance may result in a post-fire response different from that expected after burning in live stands, i.e. a compound disturbance. For example, the fire severity mosaic after burning through a live lodgepole pine forest typically consists of a mixture of patches ranging from low severity surface fire with no burning of the canopy and no tree mortality, through high severity where the canopy is consumed and trees are top-killed and/or girdled; the outcome is an increasing gradient in biomass consumed and canopy openness. In contrast, patches of low, moderate and high severity fire in a red- and grey-phase MPB-killed pine forest could all result in relatively high canopy openness because of the pre-fire death of pines and loss of canopy needles. This homogenization of post-fire canopy openness could lead to compound effects if it alters post-fire community response.

Another compound effect of short-interval disturbance could manifest if dead tree- and twig-fall from MPB killed lodgepole pines results in fire consuming a significant proportion of the aerial or surface seedbank, thereby affecting regeneration and the capacity to evade fire (Buma and Wessman, 2011). However, if lodgepole pine cones remain viable as suggested by Teste et al. (2011a), and the seedbank, whether aerial or at surface, can persist even under high intensity heat (Alexander and Cruz, 2012), subsequent fire disturbance could simply result in the expected post-fire seed release and a return to pine-dominated stands. This latter result was observed by Harvey et al. (2014a,b) who found that lodgepole pine seedling density after MPB outbreaks and fire in the green-, red-, and grey-phase, was primarily driven by seed availability and fire severity rather than pre-fire MPB outbreak severity (although they suggest the potential for compound effects in grey-phase stands where regeneration was lower).

Here, we investigate the initial successional trajectory of understory plant communities and tree regeneration in MPB-killed lodgepole pine forest along a gradient of disturbance that includes MPB alone, and MPB coupled with three levels of fire severity. Our data were generated by an experimental burn project in central interior BC that allowed us to collect pre-fire plant community data, intervene with a prescribed burn in 2006 during the late red-phase of tree death approximately 2–3 years after MPB infestation, and monitor the outcome of this intervention over five years. Our analyses focus on a comparison between pre-fire (2005/2006) and five-years post-fire (2011), examining understory community membership, community structure, and fire-adaptive traits. We define community membership, or composition as the combination of species making up the community; and community structure as the relative abundance and richness of species as displayed in rank abundance curves. Examination of plant community response to varying levels of fire severity in MPB-killed forests contributes information required to understand the long-term landscape footprint of MPB within which land management agencies will operate over the next century.

We propose three general hypotheses to be tested with our temporal comparison: (1) *The light hypothesis*. In the unburned plots, we expect that shrubs will thrive by taking advantage of canopy opening as red-phase needles fall. Increased light to the forest floor will release a greater abundance of photophilic shrubs and shade-tolerant seedlings/saplings that will overtop dwarf shrubs, low-growing vascular plants and mosses, and reduce their