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Title: Beetle Outbreaks and Wildfires: Drivers of Fire Severity, Recruitment, and Structural Legacies for Sub-boreal Forests in British Columbia.

Abstract approved: ____

Meg A. Krawchuk

Bark beetle outbreaks have left a legacy of tree mortality across fire-prone landscapes of western North America that could influence how these forests will burn and regenerate. While research has been focused on forests in the western United States, the potential interactions between mountain pine beetle (MPB) outbreaks and wildfires have yet to be investigated in the sub-boreal forests of British Columbia that have pervasive tree mortality.

In this dissertation, I explored the relationships between MPB outbreaks and wildfires through field-based approaches that evaluate the drivers of fire severity, legacy structures, and seedling recruitment, and through satellite-based approaches that evaluated the drivers of burn severity. The majority of this research focused on three fires that burned in 2012, 2013, and 2014 across two provincial parks in central interior British Columbia that are managed as wilderness, are dominated by lodgepole pine (*Pinus contorta* var. *latifolia*), and situated at the epicenter of the outbreaks in these sub-boreal forests. I examined the influence of outbreak severity on fire severity using typical first-order fire effects measured in the field as well as legacy structure related to the consumption of woody biomass on snags/trees. I evaluated post-fire seedling

recruitment across a gradient of fire severity, including fire refugia - areas only affected by MPB outbreaks and absent of recent fire. I conducted a landscape-scale assessment of MPB outbreak and fire by developing satellite maps of outbreak and fire severity to evaluate the drivers of high burn severity across these landscapes. I supplemented this research with a chemical analysis of pyrogenic carbon on snags from the Pole Creek Fire that burned through lodgepole pine forest with outbreak mortality in the eastern portion of the Cascade Range in Oregon.

In my field study, MPB outbreak severity did not influence fire severity as it related to immediate first-order fire effects, with the exception of a high probability of formation of deep char. Related to this increased formation of deep char, outbreak severity substantially influenced fire severity by affecting postfire legacy structure in these forests. My findings indicate that fire weather and topography are largely influencing fire severity related to first-order fire effects, while biomass consumption related to the architecture of structural legacies that remain post-fire is strongly linked to the status of trees at time of fire (live trees versus deadwood). These results highlight important synergistic effects of outbreak severity and fire severity. Post-fire recruitment density of lodgepole pine was related to fire severity and the abundance of serotinous cones on nearby lodgepole trees, demonstrating that fire is a key mechanism for seed release. Comparison of burned sites to fire refugia with substantial MPB outbreak mortality showed that fire is critical for regeneration of these forests. The landscape-scale assessment based on satellite data indicated that high burn severity was driven predominantly by spatial patterns in fuels and weather, with prefire vegetation conditions having the greatest relative influence on high burn severity overall. The mixture of live and dead fuels associated with post-outbreak landscapes and characterized by remote sensing indices suggested that intermediate levels of outbreak generate a fuel arrangement that supports the greatest probability of high severity fire on these landscapes.

My small field study focused on the chemical characterization of carbon legacies generated by MPB and wildfire showed that the concentration of pyrogenic carbon was higher in samples from charred snags compared to scorched snags. These findings indicate a difference in the carbon legacy that remains on landscapes where fire burns through forests with substantial prefire tree mortality versus those where fire burns through stands dominated by live trees.

Overall, this research provides insights into the disturbance and fire ecology for forests dominated by lodgepole pine with substantial prefire tree mortality from previous, recent disturbance. These forests with pervasive tree mortality burn differently than forests dominated by live trees, leaving an altered legacy structure, but dominant species, lodgepole pine, is generally resilient when MPB outbreaks and wildfire occur in short intervals. This research can inform future research and forest management as it relates to fire severity and forest resilience at the epicenter of the MPB outbreaks.

Beetle Outbreaks and Wildfires: Drivers of Fire Severity, Recruitment, and Structural Legacies for Sub-boreal Forests in British Columbia

by
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APPROVED:

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Anna C. Talucci, Author

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CONTRIBUTION OF AUTHORS

Meg A. Krawchuk assisted with study design, data analysis, and writing of Chapters 2-5. Ken P. Lertzman assisted with writing of Chapter 3. Anders J. Knudby assisted with writing of Chapter 4. Garrett W. Meigs assisted with data analysis of Chapter 4. Lauren M. Matosziuk assisted with study design, data analysis, and writing of Chapter 5. Jeff A. Hatten assisted with writing of Chapter 5. A manuscript version of Chapter 2 was accepted for publication by Ecosphere in 2019. A manuscript version for Chapter 3 is in review at Forest Ecology and Management. Manuscripts associated with Chapters 4 and 5 were in preparation for submission at the time this thesis was submitted.

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DEDICATION

To my parents, Mary and Sam Talucci, for everything.

CHAPTER ONE: INTRODUCTION

Changing disturbance regimes and the interactions among disturbances that recur across short time intervals have the potential to alter forest composition, structure, and ecosystem services. Broad-scale biotic and abiotic disturbances are projected to increase in magnitude under future climate scenarios (Dale et al. 2001, Gonzalez et al. 2010). Disturbance has been defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (White & Pickett, 1985), and this perspective is adopted throughout my dissertation. For western North American forests, recent mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreaks and current wildfire activity are creating scenarios that may foreshadow future disturbance patterns driven in part by changes in climate and provide insight into how these two disturbances may interact in time and space when they recur over short time intervals (i.e. short-interval disturbances). Short-interval disturbances may create linked effects where the first event influences the frequency or severity of the second event (Simard et al. 2011). Short-interval disturbances can also create compound effects in which the first event alters the ecological outcome of the second event, *sensu* Paine et al. (1998). When fire occurs in forests with substantial tree mortality, there is concern it may create synergistic interactions between fire and the legacy left by the MPB outbreaks that will influence postfire structural legacies, ecological response, and forest resilience (Holling 1973, Harvey et al. 2014b, Perrakis et al. 2014, Hart et al. 2015, Meigs et al. 2015, Agne et al. 2016, Johnstone et al. 2016).

The legacy of MPB outbreaks is prevalent across fire-prone landscapes of British Columbia, altering the combination of live trees and dead snags that influence the arrangement of fuels for wildfire. The extensive footprints from MPB outbreaks in British Columbia are ten times greater than what is found across the landscapes of the western United States (Raffa et al. 2008, Wulder et al. 2009). Most forests in BC affected by the current outbreak are now in the gray-phase where snags (standing dead trees) have dropped their needles (Hopkins 1909, Wulder et al. 2006, Simard et al. 2011). Recent research evaluating the interactions between beetle outbreaks and wildfire have been focused primarily in subalpine forests in the western United States (Harvey et al. 2014a, 2014b, Hart et al. 2015, Meigs et al. 2015, 2016, Agne et al. 2016), with limited focus on British Columbia (Perrakis et al. 2014) despite the widespread tree mortality from MPB outbreaks. Subalpine forests are comparable to sub-boreal forests in composition, structure, and disturbance history due to similar life zones (Holdridge 1947). However, the subalpine forest of the western United States have substantially less lodgepole pine and lodgepole pine-associated tree mortality in comparison to the sub-boreal forests in British Columbia (Wulder et al. 2009), leading to concern that what we have learned from the subalpine may not necessarily hold true for sub-boreal ecosystems. Studies in subalpine forests have evaluated the relationship between MPB outbreaks and wildfire using either field-based or satellite-based approaches generally finding minimal or no effects of outbreak severity on fire severity.

Field-based studies provide a fine-scale perspective of interactions between MPB outbreaks and wildfires. Field studies have focused on subalpine forests with predominantly lodgepole pine (Harvey et al. 2014a, Agne et al. 2016) and forests dominated by subalpine fir

(*Abies lasiocarpa*) with substantial basal area of lodgepole pine (Harvey et al. 2014b) across mountainous landscapes. Under gray-phase outbreak conditions, these studies have shown that increasing outbreak severity results in decreased subsequent fire severity (Harvey et al. 2014a, Agne et al. 2016), or limited to no effect on fire severity (Harvey et al. 2014b, Agne et al. 2016). Deep char, a metric of fire severity, was an exception that exhibited a direct positive relationship with outbreak severity (Harvey et al. 2014b). However, it is unclear if sub-boreal forests across gently rolling landscapes with more substantial tree mortality will burn differently than these subalpine forests, particularly in terms of woody biomass consumption and the structure of biological legacies of these disturbances, which have not been evaluated under the context of MPB outbreaks and wildfires.

Postfire succession has the potential to be sensitive to changes in disturbance regimes or disturbance interactions that alter ecological and structural legacies. Outbreak conditions can influence the structural and ecological legacies that persist through wildfires. For lodgepole pine forests across much of the sub-boreal and subalpine, cone serotiny, the retention of an aerial seedbank within sealed cones that are awaiting an environmental cue (Lamont et al. 1991), is a critical component for postfire regeneration of the var. *latifolia* (Lotan et al. 1985, Muir and Lotan 1985, Tinker et al. 1994), while non-serotinous lodgepole pine, var. *murrayana*, exhibit little to no recruitment postfire (Agne et al. 2016). In the decade following MPB attack, aerial seedbanks have been shown to experience a substantial reduction because as stands break down through branch breakage and tree fall cones are relocated to the forest floor (Teste et al. 2011). Stand breakdown may modify the available seedbank and the typical serotiny response to subsequent fire (Teste et al. 2011), creating the potential for an interruption of the usual cueing and postfire regeneration response, that could contribute to shifts in species composition (Johnstone et al. 2016, Stralberg et al. 2018).

Landscape-scale assessments have used satellite imagery to evaluate the influence of MPB outbreaks on wildfire events. Research has examined the effect of MPB outbreak severity on area burned under a specific temporal window of extreme fire years (Hart et al. 2015), where climate and weather would likely be a stronger driver than fuels. Other studies have evaluated relationships between outbreak activity and fire likelihood or burn severity over multiple fire years without accounting for fire weather (Meigs et al. 2015, 2016), which is a fundamental driver of fire behavior, effects, and severity. These existing studies make it challenging to infer the potential effect and/or role of outbreak severity on the fire environment and therefore on burn severity. These studies have found that outbreak severity did not influence area burned, during extreme fire years (Hart et al. 2015) or fire likelihood (Meigs et al. 2015). In additions, Meigs et al. (2016) suggest that outbreak severity dampens burn severity at the scale of the fire event for wildfires in the Pacific Northwest. These previous studies have limitations in terms of their methods and scope, as described above, but also do not share comparable conditions to those found in British Columbia together suggesting a need for further evaluation.

There is potential for post-outbreak snags to burn differently and produce more deep char on snags when compared to trees that are alive at the time of fire. While the legacy of deep char has received limited attention in the context of MPB outbreaks followed by wildfires (Harvey et al. 2014b), it has been recognized in the context of re-burns (Donato et al. 2016), when wildfire is followed by wildfire in short succession. However, deep charring has not been specifically linked with pyrogenic carbon and the carbon signatures associated with deep char in comparison to the scorching char that typically occurs when fire burns live trees. Pyrogenic carbon (PyC; referred to as soot, char, black carbon, scorch, charred biomass, deep char, and biochar) is produced from extended heating during pyrolysis of organic matter (McBeath et al. 2011, Schneider et al. 2013, Bird et al. 2015). Prolonged heating can produce high concentrations of PyC that have comparatively slower turnover times in their environment in contrast to other carbon pools (Masiello and Druffel 1998, Swift 2001, Torn et al. 2005). Understanding the concentration of PyC on snags where fire has burned through deadwood versus live trees would help to better characterize postfire legacies on landscapes with substantial prefire mortality, and form a link to biogeochemical processes operating in these forests.

Sub-boreal forests in British Columbia, Canada are an ideal region in which to study interactions between high severity beetle outbreaks and large wildfires and their influence on forest succession. In the plateau regions of the central interior, the sub-boreal forests sit on gently rolling landscapes, with forests dominated by stands of pure lodgepole pine (*Pinus contorta* var. *latifolia*), and mixtures of lodgepole pine, spruce hybrid (*Picea engelmannii x glauca*) and subalpine fir (*Abies lasiocarpa*). Species composition is driven by moisture gradients (Delong 1998) and disturbance history with lodgepole pine occupying the driest portion of the gradient with fire returns of 100-175 years, and spruce inhabiting moister pockets and/or areas with long periods without fire (Parminter 1992). Historical fire regimes tend to be infrequent, high-severity (stand-replacing) regimes (Parminter 1992). The focal region for my study was within Entiako and Tweedsmuir Provincial Parks, which are managed as wilderness and lie at the epicenter of British Columbia’s recent MPB outbreak.

This dissertation presents research to characterize the effects of MPB outbreaks followed by wildfires for lodgepole pine-dominated forests in central interior British Columbia. In the chapters that follow, I present four related studies that evaluate the effects of beetle outbreaks and wildfires on fire severity, legacy structures, and seedling recruitment through both field-based and remote sensing observations. In Chapter 2, I assess the effects of outbreak severity on fire severity based on field observations. In Chapter 3, I examine the drivers of lodgepole pine seedling recruitment across gradients of outbreak and wildfire severity. In Chapter 4, I identify the drivers of high burn severity when MPB outbreaks are followed by wildfire through a satellite-based regional assessment that complements the field perspective presented in Chapter 2. In Chapter 5, I estimate pyrogenic carbon on charred and scorched snags as it relates to wildfire burning through areas with high levels of prefire mortality for the Pole Creek Fire (2012) that burned in the Cascade Range in Oregon. These chapters address important research gaps in the disturbance ecology literature associated with a geographical region that is underrepresented and has experienced substantial mortality from MPB outbreaks. My work contributes to our understanding of fire severity, forest resilience, and carbon cycling in forests where insect outbreaks and wildfire overlap.

Literature Cited

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

Bird, M. I., J. G. Wynn, G. Saiz, C. M. Wurster, and A. McBeath. 2015. The Pyrogenic Carbon Cycle. Annual Review of Earth and Planetary Sciences 43:273–298.

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

Delong, S. C. 1998. Natural Disturbance Rate and Patch Size Distribution of Forests in Northern British Columbia : implications for Forest Management 72.

Donato, D. C., J. B. Fontaine, and J. L. Campbell. 2016. Burning the legacy? Influence of wildfire reburn on dead wood dynamics in a temperate conifer forest. Ecosphere 7:1–13.

Gonzalez, P., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Global Ecology and Biogeography 19:755–768.

Hart, S. J., T. Schoennagel, T. T. Veblen, and T. B. Chapman. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proceedings of the National Academy of Sciences of the United States of America 112:4375–80.

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecological Applications 24:1608–1625.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proceedings of the National Academy of Sciences 111:15120–15125.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367–368.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Hopkins, A. D. 1909. Practical information on the Scolytid beetles of North American forests. Page Bark beetles of the genus Dendroctonous. Washington, DC.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. W. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Lamont, B. B., D. C. Le Maitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. Botanical Review 57:277–317.

Lotan, J. E., J. K. Brown, and L. F. Neuenschwander. 1985. Role of fire in lodgepole pine forests. Pages 133–152 in D. Baumgartner, editor. Lodgepole pine the species and its management. Lodgepole pine the species and its management Symposium Proceedings, Washington State University, Pullman.

Masiello, C. A., and E. R. M. Druffel. 1998. Black carbon in deep-sea sediments. Science 280:1911–1913.

McBeath, A. V., R. J. Smernik, M. P. W. Schneider, M. W. I. Schmidt, and E. L. Plant. 2011. Determination of the aromaticity and the degree of aromatic condensation of a thermosequence of wood charcoal using NMR. Organic Geochemistry 42:1194–1202.

Meigs, G. W., J. L. Campbell, H. S. J. Zald, J. D. Bailey, D. C. Shaw, and R. E. Kennedy. 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? 6:118.

Meigs, G. W., H. S. J. Zald, J. L. Campbell, W. S. Keeton, and R. E. Kennedy. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environmental Research Letters 11.

Muir, P. S., and J. E. Lotan. 1985. Serotiny and life history of Pinus contorta var. latifolia. Canadian Journal of Botany 63:938–945.

Paine, R. T., M. J. Tegner, and E. a. Johnson. 1998. Compounded Perturbations Yield Ecological Surprises. Ecosystems 1:535–545.

Parminter, J. 1992. Typical historic patterns of wildfire disturbance by biogeoclimatic zone. Ministry of Forests, Victoria, British Columbia, Canada.

Perrakis, D. D. B., R. A. Lanoville, S. W. Taylor, and D. Hicks. 2014. Modeling Wildfire Spread in Mountain Pine Beetle-Affected Forest Stands, British Columbia, Canada. Fire Ecology 10:10–35.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. a. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. BioScience 58:501.

Schneider, M. P. W., L. A. Pyle, K. L. Clark, W. C. Hockaday, C. A. Masiello, and M. W. I. Schmidt. 2013. Toward a "molecular thermometer" to estimate the charring temperature of wildland charcoals derived from different biomass sources. Environmental Science and Technology 47:11490–11495.

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

Stralberg, D., X. Wang, M.-A. Parisien, F.-N. Robinne, P. Sólymos, C. L. Mahon, S. E. Nielsen, and E. M. Bayne. 2018. Wildfire-mediated vegetation change in boreal forests of Alberta, Canada. Ecosphere 9:e02156.

Swift, R. S. 2001. Sequestration of carbon by soil. Soil Science 166:858–871.

Talucci, A. C., and M. A. Krawchuk. 2019. Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. Ecosphere 10(5):e02744. 10.1002/ecs2.2744

Teste, F. P., V. J. Lieffers, and S. M. Landhäusser. 2011. Seed Release in Serotinous Lodgepole Pine Forests After Mountain Pine Beetle Outbreak. Ecological Applications 21:150–162.

Tinker, D. B., W. H. Romme, W. W. Hargrove, R. H. Gardner, and M. G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Canadian Journal of Forest Research 24:897–903.

Torn, M. S., P. M. Vitousek, and S. E. Trumbore. 2005. The influence of nutrient availability on soil organic matter turnover estimated by incubations and radiocarbon modeling. Ecosystems 8:352–372.

Wulder, M. a., C. C. Dymond, J. C. White, D. G. Leckie, and A. L. Carroll. 2006. Surveying mountain pine beetle damage of forests: A review of remote sensing opportunities. Forest Ecology and Management 221:27–41.

Wulder, M. A., J. C. White, D. Grills, T. Nelson, and N. C. Coops. 2009. Aerial overview survey of the mountain pine beetle epidemic in British Columbia: Communication of impacts. BC Journal of Ecosystems and Management 10:45–58.

CHAPTER 2: Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests

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Abstract

Recent regional mountain pine beetle (MPB) outbreaks have generated unprecedented tree mortality across the fire-prone landscapes of western North American forests, and could potentially modify fire severity and postfire ecological effects. In 2012, 2013, and 2014, three fires burned through high mortality, gray-phase lodgepole pine dominated forests in the plateau regions of central interior British Columbia, Canada, providing an opportunity to test for interactions between beetle outbreak and wildfire. We inventoried 63 plots that spanned gradients of outbreak severity, fire severity, and burning conditions in a wilderness setting. Our objective was to evaluate the influence of outbreak severity on fire severity by assessing typical first-order fire effects as well as legacy structure related to the consumption of woody biomass on snags/trees. We found no evidence of a relationship between outbreak severity and fire severity for six of seven first-order fire effects, with the exception of deep charring. We found evidence that legacy structure in the form of consumed branch structure and deep char development had greater odds of occurrence on MPB-killed snags compared to trees killed during wildfire. Our results indicate two key findings. First, fire severity as it relates to most first-order fire effects measures is not influenced by outbreak severity, instead more strongly influenced by the interaction of fuels, weather, and topography during fire events. Second, our results highlight how the interaction between outbreak severity and fire severity alters postfire structural legacies and their functional attributes, which could have important ecosystem implications.

Introduction

Forest ecosystems across western North America are increasingly experiencing ecological disturbances from wildfires burning through landscapes with abundant tree mortality from insect outbreaks. The recent mountain pine beetle (*Dendroctonous ponderosae*; hereafter MPB) outbreak circa the 1990s and 2000s is responsible for tree mortality in forests that span over 25 million hectares across the western United States (US) and Canada (Raffa et al. 2008, Bentz et al. 2010, Meddens et al. 2012), and British Columbia (BC) houses nearly 20 million of those hectares (Axelson et al. 2009, Perrakis et al. 2014). The spatial extent and high mortality rates associated with recent outbreaks alters standing woody fuels in affected forests from mostly alive to mostly dead, which changes the composition of the fuel profile and raises concerns for increased fire severity (Hicke et al. 2012, Jenkins et al. 2012). The overlap between MPB outbreak and wildfire disturbances that recur within a short time interval may lead to linked effects in which the first event alters the extent, severity, or probability of occurrence for the second event (Kulakowski and Veblen 2007, Simard et al. 2011). Previous field-based studies have investigated interactions of short-interval MPB-fire disturbances with variable levels of lodgepole pine (*Pinus contorta* var. *latifolia*) mortality in montane regions of the western US (Harvey et al. 2014a, 2014b, Agne et al. 2016) and found fire severity to be either weakly linked or unrelated to outbreak severity. However, the magnitude of the MPB outbreak in BC far exceeds the conditions seen in the western US (Raffa et al. 2008) and the biophysical environment differs from earlier studies (Harvey et al. 2014b, Agne et al. 2016), such that further investigation is required to understand the implications of fire burning through BC's MPB-affected forests.

The changes in fuel profiles from MPB outbreaks and subsequent stand breakdown have raised concerns among land managers for altered fire behavior and potential changes in subsequent fire severity that could generate burning conditions that are more hazardous and more severe than from fire burning through stands of live trees. Severe tree mortality alters the configuration, continuity, and moisture content of fuels over time as stands break down (i.e. needle loss, branch breakage, sloughing bark, snag fall), all of which may influence fire behavior (Page and Jenkins 2007, Hicke et al. 2012). Dry, dead fuels ignite more quickly (Stockstad 1979) and at lower temperatures (Stockstad 1975) compared to live fuels. When these dead fuels are coarse, they are prone to smoldering (Brown et al. 2003), which often extends burning time beyond the initial flaming front (Alexander 1982), thus allowing for dry dead fuels to burn longer and have more biomass consumed (Brown et al. 2003, Hyde et al. 2011) that could alter the structural legacies that persist postfire. The only known empirical study examining the effects of altered fuel profiles on fire behavior found that spread rates increased through red-phase outbreak conditions in lodgepole pine forests in BC (Perrakis et al. 2014). Simulation models posit crown fire to increase during the red-phase of outbreak conditions, 1-3 years post attack, and then decline as needles are dropped from the canopy and snags transition to gray-phase outbreak conditions, 3-10 years post attack (Hicke et al. 2012). Alternative models suggest a shift from active crown fire during the red-phase to passive crown fire in the gray-phase (Klutsch et al. 2011, Simard et al. 2011, Schoennagel et al. 2012) that could result in more biomass consumption and simplifies the legacy structure of snags.

Retrospective data that evaluates fire effects to characterize fire severity provides a complement to measures of fire behavior for understanding interactions between MPB outbreak and wildfire. Fire severity is often characterized by measurements of first-order fire effects (Reinhardt et al. 2001, Ryan and Elliot 2005), and refers to the amount of immediate ecological change associated with vegetation mortality and biomass loss from fire (Keeley 2009). Retrospective studies on MPB-fire interactions are two pronged either using remotely sensed data (e.g. satellite imagery) to quantify the amount of change between prefire and postfire conditions at coarser resolutions, or field studies that measure fire effects on the ground to characterize fire severity at finer scale resolutions. Existing remote sensing studies have shown that outbreak severity does not increase fire likelihood (Meigs et al. 2015), fire severity (Meigs et al. 2016), or area burned (Hart et al. 2015) for forests in the western US.

Field studies can capture subtleties that may be absent in remote sensing studies and have found that the relationship between outbreak severity and fire severity varies across the western US. These studies have focused on subalpine lodgepole pine forests (Harvey et al. 2014a, Agne et al. 2016) and forests dominated by subalpine fir (*Abies lasiocarpa*) but with substantial basal area of lodgepole pine (Harvey et al. 2014b) across topographically complex landscapes. Generally, these studies have suggested that gray-phase outbreak severity results in decreased fire severity (Harvey et al. 2014a, Agne et al. 2016), or limited to no change in fire severity (Harvey et al. 2014b, Agne et al. 2016) – with the exception of deep char, a metric of fire severity that showed a consistently positive relationship with severity of MPB outbreak (Harvey et al. 2014b). Some measures of fire severity increased under extreme fire weather and were attributed to burning conditions, including deep char (Harvey et al. 2014b), suggesting that prefire beetle outbreak and burning conditions contribute to deep charring on wood. Deep char is generated through incomplete combustion of deadwood often from long, smoldering burns (Bird et al. 2015) that result in more biomass consumption and is visually distinct compared to scorch that is generated from flaming combustion and typically occurs on trees that are alive at the time of fire (Campbell et al. 2007). Deep char is distinguished by its iridescent black with patterning like the scales of "alligator skin" in contrast to the matte black, dusty appearance of scorch. Deep charring on trees changes the structure and function of the postfire landscape (Campbell et al. 2007, Donato et al. 2016) by altering structural legacies, and has been clearly recognized as an important severity metric when examined in areas of high severity reburns, (fire + fire; Donato et al. 2016). However, the deep char effect, and the altered structural legacy it contributes to the postfire landscape, has largely been ignored in the context of insect outbreak and wildfire interactions.

Here, we examine the effect of gray-phase outbreak severity on fire severity for lodgepole pine dominated forests with high prefire mortality rates, in central interior BC. Our objective was to evaluate the influence of outbreak severity on fire severity by assessing first-order fire effects after three recent wildfires that burned in 2012, 2013, and 2014. We wanted to: a) ascertain whether the extensive MPB-induced tree mortality that spans the sub-boreal forests of BC responds similarly in terms of first-order fire effects to forests that have burned and been studied in the western conterminous US, and b) expand understanding and recognition of how postfire legacies (e.g., snags) can be affected by beetle outbreaks. We anticipated first-order fire effects (e.g. scorch/char height and area on trees, surface char, exposed mineral soil) would be unaffected by the severity of the outbreak and primarily driven by fire weather, based on previous findings (Harvey et al. 2014a, 2014b, Agne et al. 2016). In the context of structural legacies, we anticipated that snags killed by the MPB outbreak a decade prior to fire would burn longer, through smoldering combustion that would consume more wood biomass and lead to consistent development of deep char. We also predicted the interaction between outbreak severity and fire would reduce the structural complexity on snags, due to the potential extended duration of smoldering combustion in addition to prefire stand breakdown where MPB-killed trees experience needle loss, branch breakage, shedding of bark. In contrast, the legacies of trees that were alive at time of fire and then killed by the wildfire (i.e. fire-killed) would have less deep char and retain much more structural complexity.

Methods

Study Area

We conducted our field sampling across three fires that burned in 2012, 2013, and 2014 in Tweedsmuir and Entiako Provincial Parks, which are situated in the sub-boreal forests on the southern portion of the Nechako Plateau in BC (Figure 2.1). The study area has a mean maximum temperature of 8.5℃ (range: -3.3-19.8℃), a mean nighttime temperature of -2.8℃ (range: -11.9-6.7℃), and total annual precipitation of 507.6 mm with a monthly mean of 42.3mm (range: 22.7-60.8mm), based on the monthly means from the 1981-2010 Climate Normals data (Abatzoglou et al. 2018). Precipitation accumulates as snow in the winter and rain during the remainder of the year. Although it rains through the summer (Abatzoglou et al. 2018), there are weeks with no rain that are associated with persistent high pressure ridges (Nash and Johnson 1996). Within the fire perimeters, landscapes are associated with the Sub-Boreal Pine Spruce and Sub-Boreal Spruce biogeoclimatic zones (Meidinger and Pojar 1991), and lodgepole pine is the dominant canopy species (Figure 2.1; BCMFLNRO 2012). Moisture gradients dictate composition, structure, and disturbance history, based on historical reconstructions from surrounding areas (Steventon 2001, Francis et al. 2002) and stand age distributions (Delong 1998). Within our fire perimeters, climax lodgepole pine inhabits the driest end of the moisture gradient, seral lodgepole pine persists with mean fire returns of 100-175 years, and climax spruce (*Picea engelmannii* x *glauca*) occupies pockets with high moisture levels such as riparian zones or through succession with long intervals of no fire (Parminter 1992). The landscape is a gently rolling with low topographic relief, minimizing the topographic influence on fire behavior. Elevation ranges from 850 to 1300 m, in the region.

Field sampling occurred within three wildfire perimeters (Figure 2.1). All fires were lightning ignited and received minimal to no suppression activities due to wilderness management objectives for the parks (Rob Krause and Mike Pritchard, *personal communication*). The Entiako Lake fire (R10171) burned 7,450 ha from August 3, 2012 to September 22, 2012 (BCWS 2016). The Tweedsmuir fire (R10252) burned 3,600 ha from September 9, 2013 to September 16, 2013 (BCWS 2016). The Chelaslie River fire (R10070) burned 133,100 ha from July 8, 2014 to October 26, 2014, (BCWS 2016). All fires burned through gray-phase outbreak conditions of varying severity. The recent MPB outbreak, circa 1990s and 2000s, peaked in the region around 2003/2004, and has affected forests across much of the province (Figure 2.1). MPB activity has declined since 2006 (Wulder et al. 2009). The lag between peak outbreak and the three wildfires was about a decade, with standing dead trees (snags) beginning to transition to coarse woody debris in some outbreak affected stands. The location of fires within parks provided a rare opportunity to study MPB-fire interactions without the interference of active management (i.e. harvest/salvage activity, fire management/suppression).

Sampling Design

Field sampling occurred from late June through August 2016, allowing us to characterize a snapshot of early successional forest communities from two to four years postfire. The study area has no road access, and sampling was limited by hiking and boating distances from three remote cabins within the parks (Figure 2.1). Study plots were distributed through forest dominated by lodgepole pine. We selected plots based on a two-pronged approach including an *a priori* site selection using digital data, followed by verification and final selection in the field. *A priori* digital data included aerial survey data of MPB outbreak severity (BCMFLNRO 2016), burn severity maps generated from the differenced Normalized Burn Ratio (dNBR; Eidenshink et al. 2007), and vegetation maps from the province's Vegetation Resource Inventory to target areas of pure lodgepole pine (VRI; BCMFLNRO 2012). Aerial survey data for MPB outbreak were a coarse resolution (400m raster data products) and indicated areas within and around our study sites ranged between 50-100% canopy mortality (BCMFLNRO 2016). We selected from 12 to 39 plots in each study fire, depending on accessibility, for a total of 63 plots (Appendix S1: Table 2.S1). We distributed plots across a gradient of fire severity within each fire class based on dNBR maps as low (n=22), moderate (n=18), and high (n=23) that equated to light surface, severe surface, and crown fire based on our field measurements.

We visited plots on the ground for data collection. We verified canopy trees were predominantly lodgepole pine and were representative of the fire severity in the surrounding area. From the plot center location, we recorded GPS coordinates using a Garmin hand-held unit (GPSMAP 78s) and established a ten-by-ten-meter (100 m^2; 0.01 ha) survey plot, and divided it into four quadrants along the north–south and east–west axes, identified as NE, SE, SW, and NW. Within each quadrant, we placed a one-by-one-meter (1 m^2) subplot at increasing distances from the center of the plot (NE-1m, SE-2m, SW-3m, and NW-4m). Within plots, we recorded information for each live or dead tree: species, live/dead, evidence of MPB activity including exit holes and j-shaped galleries, diameter at breast height, and measures of first-order fire effects to characterize fire severity (including legacy structures) described in detail below. Within subplots, we recorded surface fire severity as first-order fire effects including duff depth, exposed mineral soil, terrestrial surface char, and litter. Measured variables at the plot and subplot resolution were used to characterize stand structure, MPB outbreak severity, fire severity, and to analyze the relationship between MPB outbreak and fire severity.

Mortality status of canopy trees and outbreak severity

We identified trees as live or dead at time of sampling and assigned a cause of death to each dead tree. We used these data to quantify MPB-outbreak severity, mortality from fire, and cumulative mortality for each plot. We identified a tree’s cause of death based on protocols adapted from Harvey et al. (2013, 2014a). We attributed each tree as most likely to have been: i) killed prefire by MPB (i.e. MPB-killed), ii) killed prefire by another agent (i.e. other-killed), iii) killed by fire (i.e. fire-killed), or iv) live postfire with no evidence of MPB activity (Table 2.1). We evaluated snags for MPB activity unless they were alive at time of sampling. We assessed each dead canopy tree for presence or absence of exit holes associated with adult beetles emerging from the tree (Harvey et al. 2013, 2014a). Then, we removed bark from each dead tree to identify galleries specific to MPB or other bark beetle species (Harvey et al. 2013, 2014a). We classified a tree as MPB-killed if it had the requisite exit holes and j-shaped galleries specific to MPB. While much of the prefire tree mortality present was linked to MPB, we also observed significant Ips beetle (*Ips pini*) activity, which we included as other-killed if there was no evidence of MPB. We classified a tree as other-killed if it was lacking evidence of exit holes and j-shaped galleries, but other evidence suggested death prior to fire such as no needle retention in the canopy, sloughing bark, other insect activity, and decay at the base, which is common in this system due to the moist climate (Table 2.1); this was a small portion of the total trees sampled (7%). We classified a tree as fire-killed if it had red needles in the canopy or postfire needle drop, and no evidence of prefire MPB or other beetle activity. We estimated a general metric of prefire-killed trees as the combination of MPB-killed and other-killed, (Table 2.1). We calculated plot-level metrics for outbreak severity as the proportion of MPB-killed trees per plot, and prefire mortality as the proportion of all prefire-killed trees per plot. Pre-outbreak stand estimates were based on all trees in the plot, regardless of status.

Fire severity recorded as first-order fire effects at the plot level

We characterized fire severity with seven measures of first-order fire effects that were scaled to a plot level metric. We measured fire effects on standing trees/snags and the terrestrial surface including: height of scorch and/or char on trees, percent cover of scorch and/or char on trees, percent deep charring on trees, litter/duff depth, proportion of remaining litter, proportion of terrestrial surface char, and proportion of exposed mineral soil. Scorch and deep char are visually distinct, scorch with a dusty, matte black appearance and deep char with an iridescent black, scale like appearance. In some cases, snags had both areas of scorch and deep char. The height of scorch and/or deep char (hereafter scorch/char) was measured to the nearest 0.5 m on each tree with four-meter measuring sticks and convert to mean scorch height per plot. We estimated the percent area covered, as height and circumference, of scorch and/or deep char (hereafter scorch/char) and calculated a mean proportional area per plot. We inverted the mean proportion of area per plot to the proportion of unscorched area per plot for analysis. We recorded deep char for each tree as no deep char, less than 50 percent deep char, or 50-100 percent deep char coverage on the snag and calculated the proportion of snags with deep char for a plot level variable. The four terrestrial surface fire effects metrics were measured in each subplot in the four quadrants of the plot. Litter/duff depth was measured as the combination of litter plus duff to the nearest millimeter in two opposing corners of each subplot and averaged to a plot-level variable. We recorded the percent of remaining litter, terrestrial surface char, and exposed mineral soil and calculated a mean for each variable from the four subplots to generate plot-level metric. Remaining litter, terrestrial surface char, and exposed mineral soil were converted to proportions for analysis purposes. Because we surveyed plots between two and four years postfire, we captured various early successional stages in postfire litter accumulation and vegetative regrowth.

Fire severity recorded as biomass consumption of legacy structure at the tree level

To characterize the effect of outbreaks and wildfires on postfire legacy structure, we categorized biomass loss on each tree based on the remaining branch structure and deep char.

The remaining branch structure refers to the fine, moderate, and coarse branch structure, and it was quantified as presence or absence. A classification of absence meant that there was no remaining branch structure on the tree and no associated branches on the ground in the area of the tree/snag, which indicated that branches were consumed by fire. As described above, deep char was visually distinct from scorch and recorded as absent, less than 50 percent, or 50-100 percent deep char coverage on each snag. We retained these categories to assess the relationship between deep char and remaining branch structure, and converted the categories to presence or absence of deep char for each tree/snag to evaluate the relationship between a tree's cause of death and deep char development.

Fire weather and topography

The Entiako, Tweedsmuir, and Chelaslie fires that provided the footprint for our study burned during three different fire seasons (2012, 2013, 2014) across a landscape with low topographic complexity. Fires burned over a relatively long duration within each season, which allowed us to account for variability in fire weather and day-of-burn conditions (Appendix S1: Table 2.S1). Each plot was assigned a day of burn from day-of-burn progression maps estimated from MODIS hotspot data (Parks 2014), which allowed us to assign the daily fire weather index (FWI) to each plot that was generated from the nearest weather station (Appendix S1: Table 2.S1). The calculated FWI is a metric from the Canadian Forest Fire Weather Index System (Van Wagner 1987) that integrates temperature, relative humidity, and wind speed. We used the FWI to assign each plot a burning condition category of moderate (>13–29) or extreme (>29), based on breakpoints outlined by Alexander and De Groot (1988). All fires experienced moderate burning conditions within a portion of their perimeter however, extreme burning conditions (FWI ≥ 29) only occurred in two of the three fires (2012 Entiako and 2014 Chelaslie fires; Appendix S1: Table 2.S1). For plots, elevation fluctuated between 873 to 1043 m. Plots were relatively flat with a mean slope of 2.6 degrees (range: 0-20 degrees). We did not pursue topography as an explanatory variable of fire severity due to the low topographic variability at our study plots.

Statistical Analysis

We tested for relationships between each of the seven fire effects metrics and MPB outbreak severity at the plot-level, while accounting for burning conditions. Our seven fire effects metrics served as response variables: average scorch/char height, average proportion of unscorched/uncharred area on trees, proportion of trees with deep char, litter/duff depth, proportion of remaining litter, proportion of terrestrial surface char, and proportion of exposed mineral soil. We tested the relationship of each response variable against the proportion of MPB-killed trees (our index of MPB severity) and burning conditions, which was included as a categorical variable of moderate or extreme FWI (Appendix S1: Table 2.S1). An interaction term between burning conditions and proportion of MPB-killed trees was included in all models to assess whether observed relationships changed under different fire weather conditions. Relationships with scorch/char height and litter/duff depth were fit using linear models. The proportion of terrestrial surface char was logit transformed and fit with a linear model. All other models in which the response variable was a proportion were analyzed with generalized linear models, and each response variable was fit with a distribution appropriate for the type and distribution of the response variable (see Appendix S1: Table 2.S3 for distributions associated with each analysis). We also ran each model and replaced the proportion of MPB-killed trees with the proportion of prefire-killed trees, since dead trees would all be similar in terms of conditions and moisture content regardless of what killed them. The models with the proportion of prefire-killed trees demonstrated similar statistical relations to the proportion of MPB-killed trees. We report all models that were statistically significant, and we kept all fire effects models that were run with the proportion of MPB-killed trees as an explanatory variable, since these models were a more conservative estimate of MPB caused mortality.

We evaluated the effect of outbreak severity and wildfire on postfire legacy structure from tree-level fire effects of deep char and branch structure loss. We analyzed data at the tree-level using two different response variables: 1) presence/absence (1/0) of branch structure on individual trees and 2) presence/absence (1/0) of deep char on individual trees. We accounted for burning conditions as a categorical variable of moderate or extreme FWI (Appendix S1: Table 2.S1). An interaction term between burning conditions and cause of death was included in all models. We used generalized linear mixed models with a binomial distribution for presence/absence data using a logit link, and each model included the plot as a random effect and the interaction term between cause of death and burning conditions. Results are reported as probability of occurrence, and the comparison between mortality types (e.g., MPB-killed versus fire-killed) is reported as the odds ratio. Additionally, we determined whether the presence/absence of branch structure was related to the coverage of deep char on the tree. Our explanatory variable of deep char was treated as a three-level categorical variable of no deep char, less than 50% coverage of deep char, or 50-100% coverage of deep char on the tree, while accounting for burning conditions.

We assessed fit for all models by visually inspecting the residuals, which appeared to be adequately met. We evaluated and corrected for overdispersion in all generalized linear models and generalized linear mixed models when necessary. For our two linear models, assumptions of normality and constant variance of the residuals were checked graphically and appeared to be adequately met. We assessed the interaction term with a drop-in-deviance test. The interaction term was retained in each model regardless of statistical significance, because of the known interaction between fire weather and fuels. All statistical analyses were conducted in R statistical computing software version 3.4.4 with the stats package (R Development Team 2018). For generalized linear models we used the function 'glm' in the MASS package (Venables and Ripley 2002). For generalized linear mixed models we used the function 'glmer' in the lme4 package (Bates et al. 2015). We considered $p < 0.05$ as convincing evidence of a relationship and $p < 0.10$ as suggestive of a relationship to minimize the potential of a Type II error. Data and code for analyses are available online (Talucci 2019).

Results

We collected data from 943 trees across 63 field plots with 910 lodgepole pine trees/snags and 33 spruce trees/snags. Canopy tree species were predominantly lodgepole pine with a plot mean of 96% (range across plots: 63-100%, Appendix S1: Table 2.S2). Estimated mortality from MPB was 59% of all trees sampled, and estimated prefire mortality (i.e. MPB-killed plus other-killed) was 66% of all trees sampled (Table 2.1). When we evaluated just lodgepole pine mortality across all 63 plots, the estimated mean for lodgepole pine killed by MPB was 63% and the estimated mean for lodgepole pine killed by all agents prior to fire (all prefire) was 70% (Appendix S1: Table 2.S2). Cumulative mortality was estimated at 93% for lodgepole pine as a combination of prefire and fire mortality (Appendix S1: Table 2.S2).

Effect of outbreak severity on first-order fire effects at the plot level

The effect of outbreak severity on fire severity was limited, with six of seven fire effects showing no evidence of an effect (Figure 2.2, Appendix S1: Table 2.S3). average scorch/char height, average proportion of unscorched/uncharred area on trees, litter/duff depth, proportion of remaining litter, proportion of terrestrial surface char, and proportion of exposed mineral soil showed no evidence of an effect of outbreak severity (Figure 2.2, Appendix S1: Table 2.S3). Outbreak severity did show evidence of an effect on proportion of trees with deep char. Under moderate burning conditions, the proportion of trees with deep char increased with increasing outbreak severity (Figure 2.2, Appendix S1: Table 2.S3), which held true when we substituted the proportion of prefire-killed trees for MPB-killed trees (Figure 2.2, Appendix S1: Table 2.S3). Under extreme burning conditions the relationship between the proportion of MPB-killed trees and deep char was not statistically significant, however when we substituted the proportion of prefire-killed trees for MPB-killed trees that relationship was statistically significant (Figure 2.2, Appendix S1: Table 2.S3).

Effect of outbreak and wildfire on legacy structure

Outbreak severity and wildfire showed distinct evidence of an effect on the legacy structure of the forest, measured by biomass consumption as deep char and branch structure loss on individual trees. Both deep char development and branch structure loss had greater odds of occurrence when a tree was dead prior to fire (i.e. MPB-killed or prefire-killed) compared to being alive at time of fire, which was consistent across both moderate and extreme burning conditions (Figures 2.3 & 2.4, Appendix S1: Table 2.S4). Under both moderate and extreme burning conditions, a MPB-killed and prefire-killed snag had greater odds of developing deep char compared to a fire-killed tree (Figure 2.3 & 2.4, Appendix S1: Table 2.S4). There were greater odds of branch structure being consumed on a MPB-killed and prefire-killed snag compared to a fire-killed tree under moderate conditions, and the size of that effect was slightly smaller under extreme conditions but still significant (Figure 2.3 & 2.4, Appendix S1: Table 2.S4). We found that branch structure had greater odds of being consumed when deep char exceeded 50% coverage on the tree for both moderate and extreme burning conditions (Figure 2.5, Appendix S1: Table 2.S5).

Discussion

We found that fire severity as measured by scorch/char height and area, and surface fire metrics, is not influenced by MPB outbreak severity but that fire severity measured as biomass loss and legacy structure was consistently influenced by the outbreak history. These findings from British Columbia align with previous field research that evaluated the influence of outbreak severity on fire severity in the western US (Harvey et al. 2014a, 2014b, Agne et al. 2016), but extends our understanding of these short-interval disturbances by highlighting the synergistic effect on postfire structural legacies. Prefire mortality had a greater likelihood for increased biomass consumption and deep char, which aligns with findings on reburns, where wildfires recur in short intervals (Donato et al. 2016). Prefire mortality, regardless of the mechanism of death, results in an altered legacy structure that is more simplistic and has more deep char. While this effect on structural legacies is generally accepted in the field, it has been broadly overlooked and unquantified in assessments of how outbreak affects fire severity. When asking the question “does MPB outbreak affect fire severity, are they linked disturbances”, the answer is yes – specifically through the deadwood structure that remains in these ecosystems.

Effect of outbreak severity on first-order fire effects at the plot level

Outbreak severity did not show evidence of an effect on fire severity for six out of seven measured first-order fire effects; the exception was deep char. This reflects similar findings in gray-phase outbreak conditions found by Harvey et al. (2014b) and extends our understanding to the geography of British Columbia’s sub-boreal forests. Our finding indicates some inherent noise and uncertainty in our data as well as the influence of fire weather. The six fire effects – scorch/char height and area, duff depth, litter, surface char, and exposed soil, are likely controlled by the combined factors of the fire environment, i.e. the interaction of fuels, weather, and topography (Countryman 1972, Krawchuk and Moritz 2011, Whitman et al. 2015) but without a strong signal from outbreak fuel structure, which aligns with previous research evaluating interactions between outbreak severity and fire severity (Harvey et al. 2014a, 2014b, Agne et al. 2016). Scorch on trees is naturally variable and can be driven by multiple factors including the composition of fuel structures, crown and/or surface fire spread, burning conditions, slope steepness, and ignition patterns (Alexander and Cruz 2012a). Our results show no evidence of a relationship between terrestrial surface fire effects and outbreak severity, which was also consistent with findings in previous retrospective studies with gray-phase outbreak conditions (Harvey et al. 2014b, Agne et al. 2016). The lag time between needle drop and our study fires would have allowed for the decomposition of fine fuels (Simard et al. 2011, Harvey et al. 2013) thus minimizing the effect of outbreak on surface fuels. Most snags were still standing at time of fire, so that the concern of increased surface fire severity from abundant coarse woody debris was not observed. These findings support the general narrative that low-frequency and high-severity fire regimes associated with lodgepole pine in sub-boreal forests are strongly driven by climate systems of high-pressure, creating dry-hot conditions conducive for burning such that variability in fuel structure/vegetation plays a secondary role (Bessie and Johnson 1995, Nash and Johnson 1996, Whitman et al. 2015).

Effect of outbreak and wildfire on structural legacies

Our findings support the notion that dead wood, which in our landscapes is predominantly snags generated by MPB outbreak, burns differently than live wood and indicates an important MPB-fire connection. Live trees rarely experience significant combustion and therefore little to no consumption occurs on the tree (Campbell et al. 2007), which is attributed to higher moisture content compared to their dead counterparts (Brown et al. 1985). Extended periods of smoldering and glowing combustion (Brown et al. 1985, Page and Jenkins 2007, Hyde et al. 2011) are facilitated by lower moisture content in snags and coarse wood (Stockstad 1979).

Lower moisture content in snags could enable passive crown fire or torching of snags (Wenger 1984), which may be the primary mechanism for consumption of branch structure. Some simplification of branch structure may also occur on gray-phase MPB killed trees prior to fire. The torching of snags and extended periods of smoldering have been demonstrated in areas that experience reburn, wildfires that recur in short intervals (Donato et al. 2016). High severity reburns have shown there is an eight-fold increase in deep char development on snags and the retention of woody biomass is half the amount of once burned areas, in the Klamath Mountains of southwestern Oregon (Donato et al. 2016). Where wind-throw is followed by wildfire in short intervals, snags and coarse wood has been shown to be reduced with marginal increase in charred material (Buma et al. 2014). In lodgepole pine/Douglas-fir (*Pseudotsuga menziesii*) forests on the Chilcotin Plateau of BC south of our study sites, areas of high prefire mortality from MPB outbreak experienced 13 percent more consumption of dead wood and the variability in canopy consumption was attributed to mortality status with dead prefire snags having more of their branch structure consumed (Brad Hawkes, *personal communication*). This evidence indicates that it is not necessarily the mechanism of prefire mortality, e.g. MPB outbreak, wind-throw, or prior wildfire, but the fact that there is an abundance of deadwood with altered moisture levels and fuel structure compared to live wood, which alters postfire ecological and structural legacies as they relate to standing snags and coarse woody debris.

The consumption of branches and deep char development on snags alters the structural legacies that endure through fire. These altered legacies may introduce long-term implications for ecosystem structure and function including availability of canopy seedbank, accumulation of coarse woody debris, and early seral structure and resources for early seral species (Franklin et al. 2000, Swanson et al. 2011, Johnstone et al. 2016). After MPB outbreak, lodgepole pine snags continue to retain some their aerial seedbank in the canopy postmortem while some cones fall to the forest floor (Teste et al. 2011). Cones in snags or on the forest floor can be exposed to extended heating from a snag smoldering or slower moving surface fire (Alexander and Cruz 2012b), which could reduce seedbanks and influence postfire resilience (Johnstone et al. 2016). The loss in snag biomass and branch structure alters the accumulation of coarse wood that may influence short- and long-term carbon and nutrient cycles (Harmon 2001), structure of habitat for wildlife (Fontaine et al. 2009, House 2014) including nesting and perching habitat, and both structure and function of early seral ecosystems (Swanson et al. 2011). More charring on trees reduces the quality of the snag for saproxylic insects thereby affecting foraging woodpeckers (Saint-Germain et al. 2004, Nappi et al. 2010), which could influence trophic webs. Deep char development can encapsulate the remaining wood, which may limit decomposition, slow decay, and extend long-term carbon storage (Preston 2009, Bird et al. 2015). Together, these changes to dead wood that may alter the long-term structure and function in the postfire forest are considered compound disturbance effects, where the outbreak severity and fire severity work in combination to create unique post-disturbance conditions that are different then the outcomes of the singular disturbance of wildfire (Paine et al. 1998). Further research is needed to determine the long-term implications of compound disturbance effects related to legacy structure, coarse wood recruitment, carbon storage, pyrogenic carbon, habitat structures, trophic webs, and early seral ecosystems in forests where fires are increasingly burning through stands with high volumes of snags from insects, wind-throw, drought, and prior fire.

Conclusion

Sub-boreal forest ecosystems of BC have experienced widespread tree mortality from the MPB outbreak, generating a fuel structure characterized by an abundance of deadwood that is now interacting with wildfires. The contiguous landscape of lodgepole pine dominated forests situated at the epicenter of the outbreak in western North America allowed us to assess interacting, or linked, effects between outbreak and fire severity. Our results suggest that while many first-order fire effects are not influenced by outbreak severity, legacy structure related to the degree of biomass consumption is strongly influenced by the interaction of outbreak severity and fire severity. These findings are especially important to consider after the 2017 and 2018 fire seasons in BC wherein a record number of hectares burned, with many of the fires burning through snag forests affected by MPB outbreaks.

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Literature Cited

Abatzoglou, J. T., S. Z. Dobrowski, S. A. Parks, and K. C. Hegewisch. 2018. Terraclimate, a high-resolution global dataset of monthly climate and climate water balance from 1958-2015. Scientific Data.

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

Alexander, M. E. 1982. Calculating and interpreting forest fire intensities. Canadian Journal of Botany 60:2185–2185.

Alexander, M. E., and M. G. Cruz. 2012a. Interdependencies between flame length and fireline intensity in predicting crown fire initiation and crown scorch height. International Journal of Wildland Fire 21:95–113.

Alexander, M. E., and M. G. Cruz. 2012b. Modelling the impacts of surface and crown fire behavior on serotinous cone opening in jack pine and lodgepole pine forests. International Journal of Wildland Fire 21:709–721.

Alexander, M. E., and W. J. De Groot. 1988. Fire Behavior in Jack Pine Stands as related to the Canadian Forest Fire Weather Index (FWI) System. Canadian Forestry Service, Northwest Region, Edmonton, Alberta, Canada.

Axelson, J. N., R. I. Alfaro, and B. C. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. Forest Ecology and Management 257:1874–1882.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

BCMFLNRO. 2012. Vegetation Resources Inventory. British Columbia Ministry of Forests Lands and Natural Resource Operations, Victoria, BC, Canada.

BCMFLNRO. 2016. Aerial Overview Survey Data Files. https://www2.gov.bc.ca/gov/content/environment/research-monitoring-reporting/monitoring/aerial-overview-surveys/data-files.

BCWS. 2016. Historical Fire Perimeters. British Columbia Wildfire Service, Victoria, BC.

Bentz, B. J., J. Regniere, C. J. Fettig, M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. Negron, and S. J. Seybold. 2010. Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects. BioScience 60:602–613.

Bessie, W. C., and E. A. Johnson. 1995. The Relative Importance of Fuels and Weather on Fire Behavior in Subalpine Forests. Ecology 76:747–762.

Bird, M. I., J. G. Wynn, G. Saiz, C. M. Wurster, and A. McBeath. 2015. The Pyrogenic Carbon Cycle. Annual Review of Earth and Planetary Sciences 43:273–298.

Brown, J. K., M. A. Marsden, K. C. Ryan, and E. D. Reinhardt. 1985. Predicting Duff and Woody Fuel Consumed by Prescribed Fire in the Northern Rocky Mountains. Research Paper INT-337.

Brown, J. K., E. D. Reinhardt, and K. A. Kramer. 2003. Coarse woody debris: managing benefits and fire hazard in the recovering forest. USDA Forest Service Gen. Tech. Rep. 105:1–16.

Buma, B., R. E. Poore, and C. A. Wessman. 2014. Disturbances, Their Interactions, and Cumulative Effects on Carbon and Charcoal Stocks in a Forested Ecosystem. Ecosystems

17:947–959.

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research: Biogeosciences 112:1–11.

Countryman, C. M. 1972. The fire environment concept. Berkeley, CA.

Delong, S. C. 1998. Natural Disturbance Rate and Patch Size Distribution of Forests in Northern British Columbia : lmplications for Forest Management 72.

Donato, D. C., J. L. Campbell, J. B. Fontaine, and B. E. Law. 2009. Quantifying char in postfire woody detritus inventories. Fire Ecology 5:104–115.

Donato, D. C., J. B. Fontaine, and J. L. Campbell. 2016. Burning the legacy? Influence of wildfire reburn on dead wood dynamics in a temperate conifer forest. Ecosphere 7:1–13.

Eidenshink, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, S. Howard, S. Falls, and S. Falls. 2007. A Project for Monitoring Trends in Burn Severity. Fire Ecology 3:3–21.

Fontaine, J. B., D. C. Donato, W. D. Robinson, B. E. Law, and J. B. Kauffman. 2009. Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. Forest Ecology and Management 257:1496–1504.

Francis, S. R., S. Skinner, M. Gallagher, and C. Marion. 2002. Characterising fire regimes: Fire history research in the SBPS and SBS biogeoclimatic zones of the Cariboo Forest Region. Williams Lake, British Columbia, British Columbia.

Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. Mckee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity: Ecosystem disturbances, biological legacies and ecosystem recovery. Conservation in Practice 1:8–17.

Harmon, M. E. 2001. Moving Towards a New Paradigm for Woody Detritus Management. Ecological Bulletins 49:269–278.

Hart, S. J., T. Schoennagel, T. T. Veblen, and T. B. Chapman. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proceedings of the National Academy of Sciences of the United States of America 112:4375–80.

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

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecological Applications 24:1608–1625.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proceedings of the National Academy of Sciences 111:15120–15125.

Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

House, K. N. 2014. Bird and beetle assemblages in mountain pine beetle killed forests and those subsequently burned: evidence for an effect of compound natural disturbances in British Columbia. Simon Fraser University.

Hyde, J. C., A. M. S. Smith, R. D. Ottmar, E. C. Alvarado, and P. Morgan. 2011. The combustion of sound and rotten coarse woody debris: A review. International Journal of Wildland Fire 20:163–174.

Jenkins, M. J., W. G. Page, E. G. Hebertson, and M. E. Alexander. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in Western North America and implications for fire management. Forest Ecology and Management 275:23–34.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. W. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Klutsch, J. G., M. A. Battaglia, D. R. West, S. L. Costello, and J. F. Negron. 2011. Evaluating Potential Fire Behavior in Lodgepole Pine-Dominated Forests after a Mountain Pine Beetle Epidemic in North-Central Colorado. Western Journal of Applied Forestry 26:101–109.

Krawchuk, M. A., and M. A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. Ecology 92:121–132.

Kulakowski, D., and T. T. Veblen. 2007. Effect of Prior Disturbances on the Extent and Severity of Wildfire in Colorado Subalpine Forests. Ecology 88:759–769.

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

Meigs, G. W., J. L. Campbell, H. S. J. Zald, J. D. Bailey, D. C. Shaw, and R. E. Kennedy. 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? 6:118.

Meigs, G. W., H. S. J. Zald, J. L. Campbell, W. S. Keeton, and R. E. Kennedy. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environmental Research Letters 11.

Nappi, A., P. Drapeau, M. Saint-Germain, and V. A. Angers. 2010. Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. International Journal of Wildland Fire 19:500–511.

Nash, C. H., and E. A. Johnson. 1996. Synoptic climatology of lightning-caused forest fires in subalpine and boreal forests. Canadian Journal of Forest Research 26:1859–1874.

Page, W. G., and M. J. Jenkins. 2007. Predicted fire behavior in selected mountain pine beetle infested lodgepole pine. Forest Science 53:662–674.

Paine, R. T., M. J. Tegner, and E. a. Johnson. 1998. Compounded Perturbations Yield Ecological Surprises. Ecosystems 1:535–545.

Parks, S. A. 2014. Mapping day-of-burning with coarse-resolution satellite fire-detection data. International Journal of Wildland Fire 23:215.

Parminter, J. 1992. Typical historic patterns of wildfire disturbance by biogeoclimatic zone. Minsitry of Forests, Victoria, British Columbia, Canada.

Perrakis, D. D. B., R. a. Lanoville, S. W. Taylor, and D. Hicks. 2014. Modeling Wildfire Spread in Mountain Pine Beetle-Affected Forest Stands, British Columbia, Canada. Fire Ecology 10:10–35.

Preston, C. M. 2009. Fire’s black legacy. Nature Geoscience 2:674–675.

R Development Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. a. Hicke, M. G. Turner, and W. H.

Romme. 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. BioScience 58:501.

Reinhardt, E. D., R. E. Keane, and J. K. Brown. 2001. Modeling fire effects. International Journal of Wildland Fire 10:373–380.

Ryan, K., and W. J. Elliot. 2005. Fire effects and soil erosion models. Pages 171–177 *in* D. G. Neary, K. C. Ryan, and L. F. DeBano, editors. Wildland fire in ecosystems: effects of fire on soils and water. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.

Saint-Germain, M., P. Drapeau, and C. Hébert. 2004. Xylophagous insect species composition and patterns of substratum use on fire-killed black spruce in central Quebec. Canadian Journal of Forest Research 685:677–685.

Schoennagel, T., T. T. Veblen, J. F. Negron, and J. M. Smith. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE 7:1–14.

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

Steventon, J. D. 2001. Morice Timber Supply Area Timber Supply Review. Smithers, British Columbia, British Columbia.

Stockstad, D. S. 1975. Spontaneous and piloted ignition of pine needles. Ogden, Utah.

Stockstad, D. S. 1979. Spontaneous and Piloted Ignition of Rotten Wood. Ogden, Utah.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.

Talucci, A. C. 2019. Data and code: Outbreak and Wildfire Severity BC (Version v1.0.0) [Data set]. Ecosphere. Zenodo. http://doi.org/10.5281/zenodo.2648051

Teste, F. P., V. J. Lieffers, and S. M. Landhäusser. 2011. Seed Release in Serotinous Lodgepole Pine Forests After Mountain Pine Beetle Outbreak. Ecological Applications 21:150–162.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Springer, New York.

Van Wagner, C. E. 1987. Development and structure of the Canadian forest fire weather index system. Page Forestry Technical Report 35. Ottawa.

Wenger, K. F. 1984. Fire Management. Page 220 Forestry Handbook. John Wiley & Sons, New York.

Whitman, E., E. Batllori, M.-A. Parisien, C. Miller, J. D. Coop, M. A. Krawchuk, G. W. Chong, and S. L. Haire. 2015. The climate space of fire regimes in north-western North America. Journal of Biogeography 42:1736–1749.

Wulder, M. A., J. C. White, D. Grills, T. Nelson, and N. C. Coops. 2009. Aerial overview survey of the mountain pine beetle epidemic in British Columbia: Communication of impacts. BC Journal of Ecosystems and Management 10:45–58.

Tables

Table 2.1. The criteria and classes used to identify a tree's cause of death for the study region in BC. Methods adapted from Harvey et al. (2014a). Trees sampled summarizes observed data from field collections.

Cause of Death	Description	Trees Sampled (%)
Live tree	Live when sampled; green canopy; no visible beetle activity	4.67
Fire-killed	Dead when sampled; scorched bark, branches, and/or outer sapwood; no evidence of galleries or exit holes from MPB or other bark beetle activity; not highly decayed/weathered particularly at the base and in the canopy	28.95
MPB-killed	Dead when sampled; no needles remaining in the canopy; vacated mountain pine beetle (MPB) galleries in cambium with exit holes in remaining bark	59.38
Other-killed	Dead when sampled; highly decayed/weathered, no bark, missing branches; more advanced decay then MPB-killed trees; full deep char with no identifiable vacated MPB galleries	7.00
Prefire-killed: MPB-killed + Other-killed	All prefire-killed from both MPB-killed and other-killed	66.38

Figures

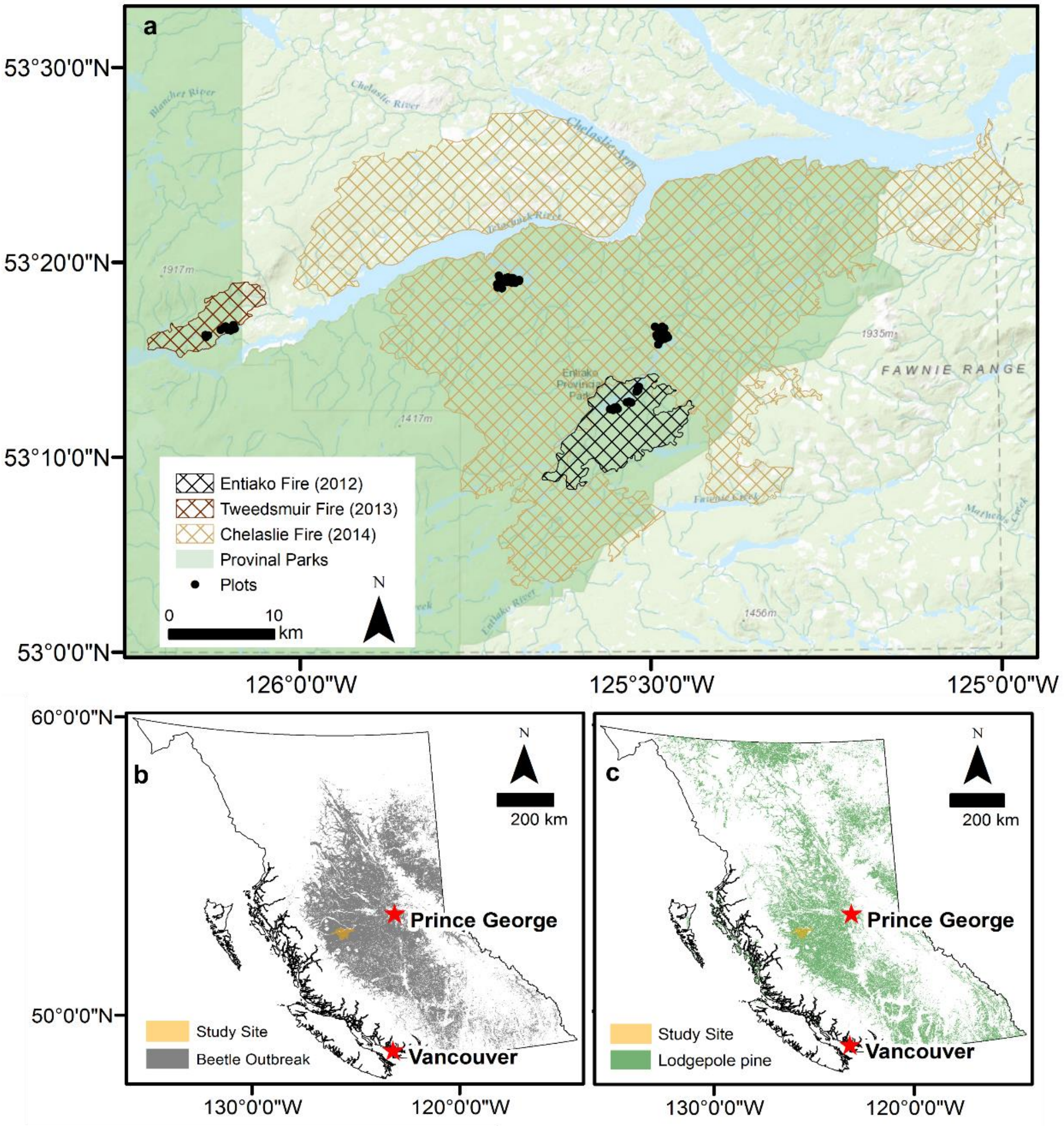

Figure 2.1. Maps of the study area, MPB outbreak extent, and lodgepole pine range. Fire perimeters for three study fires that burned in 2012 (Entiako Fire; 7,459 ha), 2013 (Tweedsmuir Fire; 3,354 ha), and 2014 (Chelaslie Fire; 133,000 ha). Panel **a**, provincial park boundaries are displayed as protected areas and overlaid with fire perimeters. Panel **b** shows the extent of the MPB outbreak across British Columbia based on aerial survey data from 2000-2011 (BCMFLNRO 2016). Panel **c**, shows the estimated range of lodgepole pine across British Columbia.

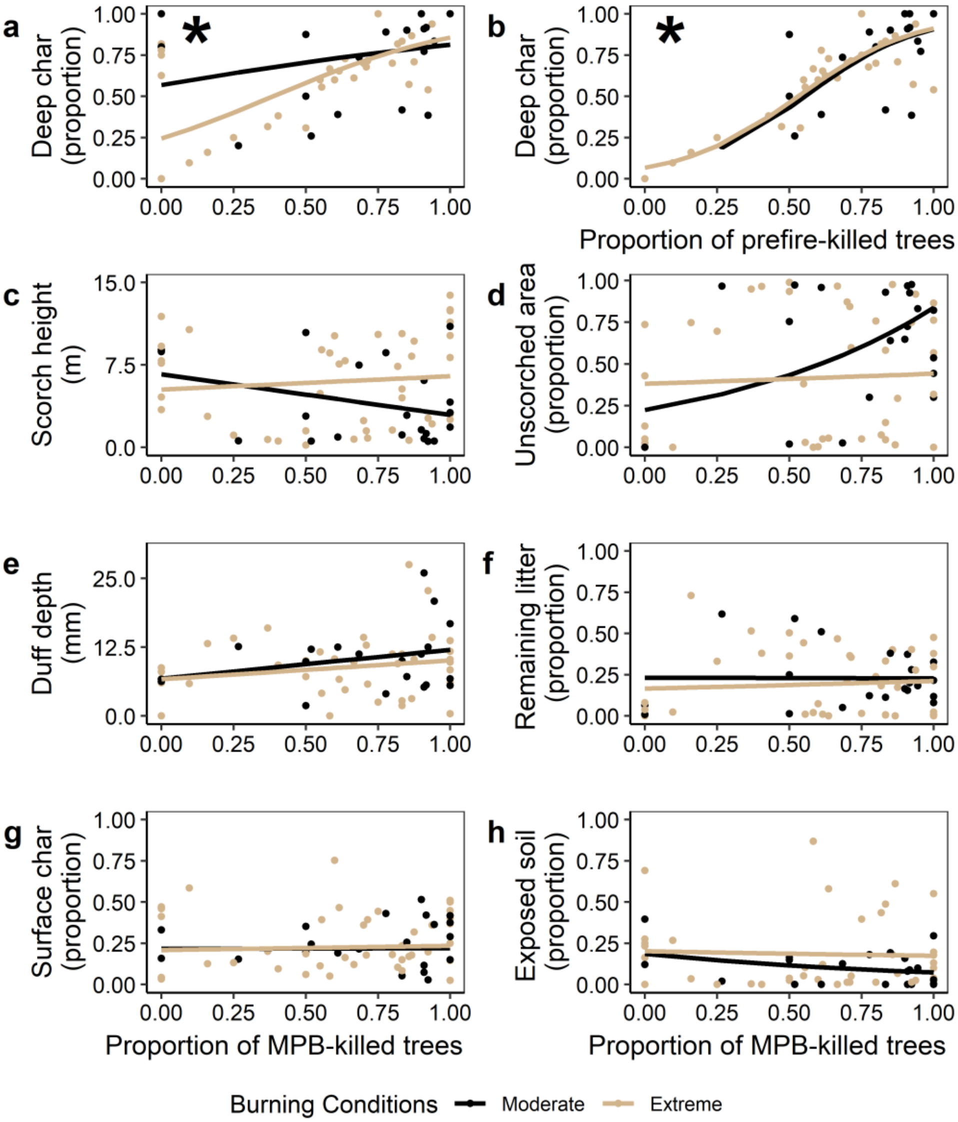

Figure 2.2. The relationships between outbreak severity and seven first-order fire effects measured at the plot-level: proportion of trees with deep char (**a**-**b**), average scorch/char height (**c**), average proportion of unscorched/uncharred area on trees (**d**), litter/duff depth (**e**), proportion of remaining litter (**f**), proportion of terrestrial surface char (**g**), and proportion of exposed mineral soil(**h**). Response variables are along the y-axis with the explanatory variable of the proportion of mountain pine beetle (MPB) killed trees or prefire killed trees (only panel **b**) along the x-axis. Points are the raw data (n=63 plots), and fitted lines show the estimated statistical relationship. The response variable of deep char is shown in panels **a** and **b**, and they were the only two models that indicated a strong statistical relationship (*****). Response varaible **c**-**h** were unrelated to outbreak severity. See Appendix S1: Table 2.S3 for model estimates and confidence intervals.

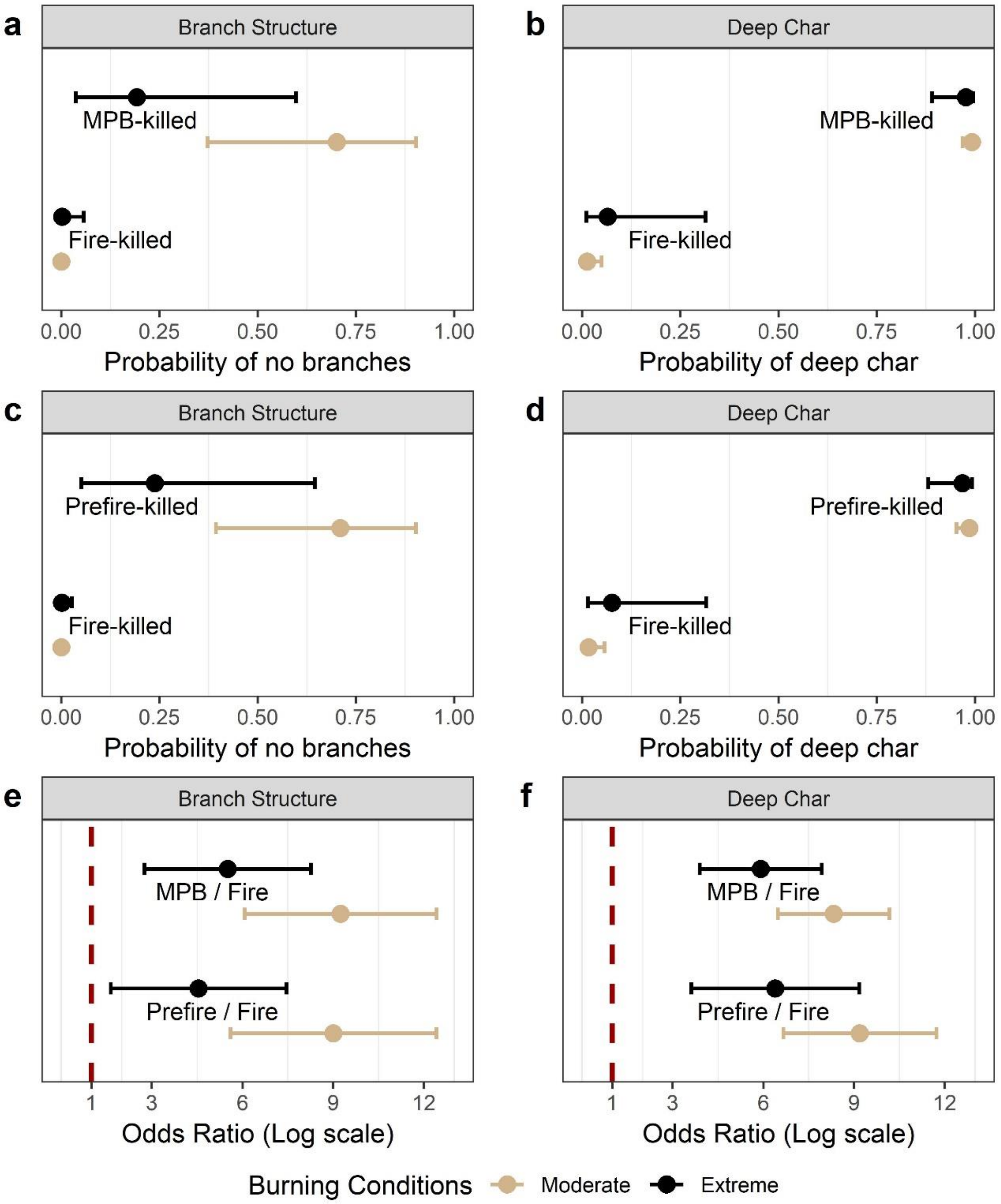

Figure 2.3. The effect of outbreak severity and wildfire on legacy structure measured at the tree-level. Tree-level fire effects show the role of mountain pine beetle (MPB) outbreak severity (MPB-killed and prefire-killed) on consumption of woody material and simplification of structural legacies in the form of branch loss and deep char development (**a-d**). Comparison between groups (i.e. MPB-killed versus fire-killed) are shown in **e** and **f** as odds ratios with the red dashed line marking no difference at one. The model estimates are listed in Appendix S1: Table 2.S4.

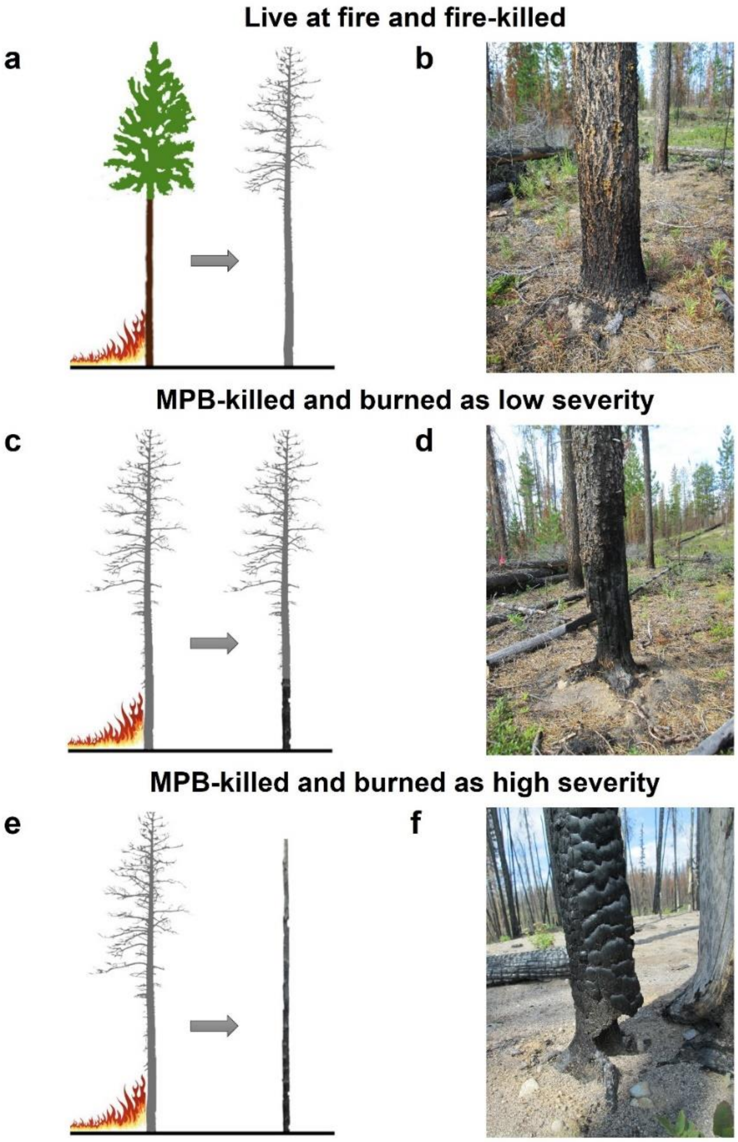

Figure 2.4. Tree-level fire effects are dependent on whether a tree is alive or dead at time of fire. Panel **a** illustrates a tree that is live at time of fire and killed by fire, with the adjacent panel **b** showing a photo of a tree live at time of fire and killed by fire with scorched bark but no consumption of the tree. Panel **c** illustrates a MPB-killed tree that burns under low severity conditions, with the adjacent panel **d** showing a photo of deep char development and consumption at the base of the tree, which is attributed to fungal development (Donato et al. 2009). Panel **e** illustrates a MPB-killed tree that burns under high severity conditions, with the adjacent panel **f** showing a photo of deep char that covers the entire tree in a plot that burned as high severity.

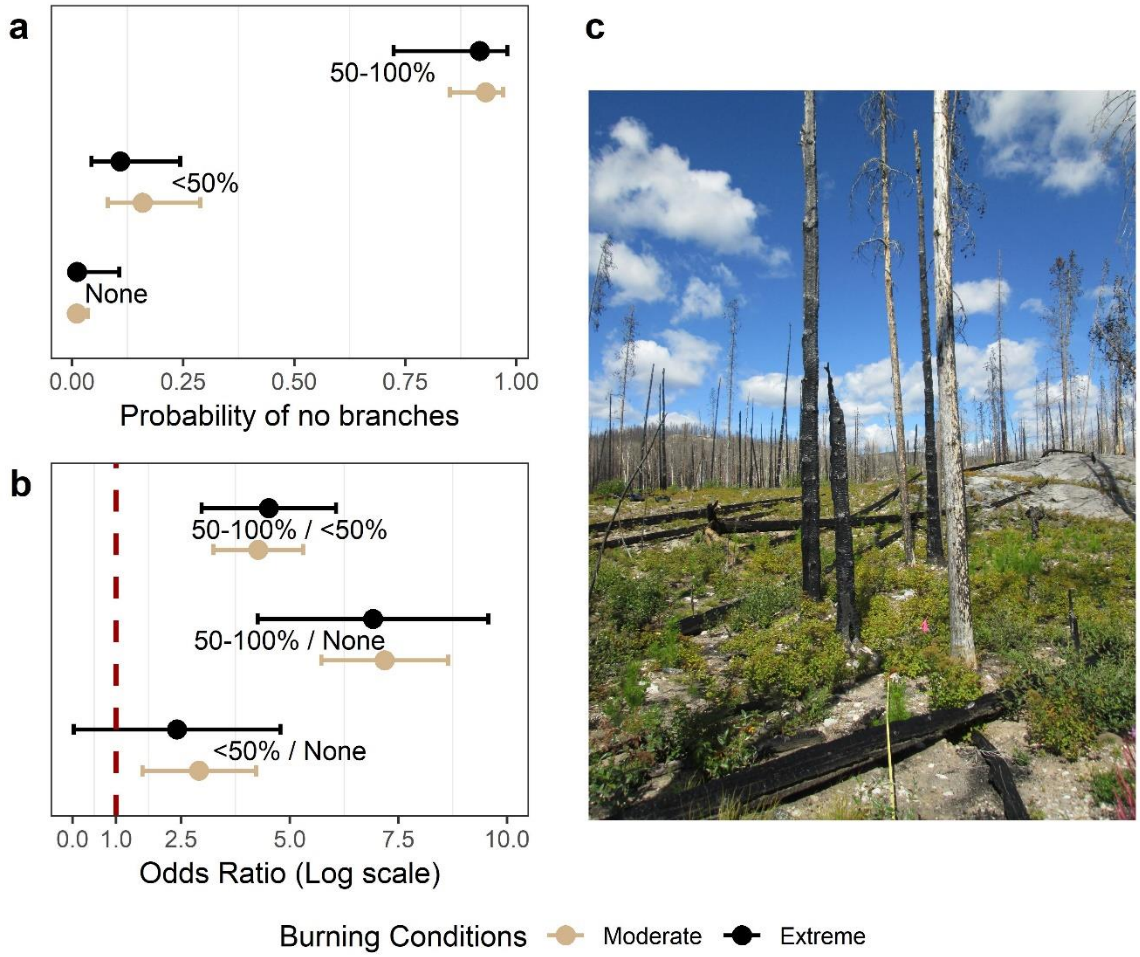

Figure 2.5. Deep char coverage influences the consumption of branch structure on a tree. The probability of branch loss from deep char development is shown in **a**. Comparisons between groups are shown in **b** with a red dashed line demarcating no difference at one. In **c**, a photo of a snag with deep char and no branches adjacent to a snag with branches still intact and no deep char. Model estimates are list in Appendix S1: Table 2.S5.

Appendix

Table 2.S1. Regional weather conditions for classifying moderate and extreme burning conditions. Break points for moderate and extreme burning conditions are based on the Fire Weather Index (FWI) following Alexander and De Groot (1988). Burning Conditions were assigned based on the FWI with ≥ 29 as extreme burning conditions and < 29 as moderate burning conditions. We acquired weather station data from the nearest weather station with a complete data set for the fire season for each fire. Weather data for R10170 and R10252 came from the Moose Lake and Nadina BC Wildfire Active Weather Station System respectively. Weather data for R10070 came from the Ootsa Lake–Skins Lake BC Climate Station System. Day of burn was assigned to each field plot from day-of-burn progression maps (Parks 2014), generated from MODIS hotspot data (NASA MCD14ML product, Collection 5).

Fire Name (Fire ID)	Area Burned (ha)	Burning Conditions	No. of Plots	FWI	Relative Humidity (%)	Temperature (°C)	Wind Speed (m/s)
	Date start-end			Mean (Range)	Mean (Range)	Mean (Range)	Mean (Range)
Entiako (R10171)	7,459	Moderate	4	22.3 (15.1-26.0)	38.3 (28.0-54.0)	22.5 (14.6-28.2)	8.3 (4.2-13.2)
	2012/08/03-2012/09/22	Extreme	8	34.6 (29.6-38.2)	29.3 (22.0-40.0)	22.6 (15.0-26.8)	8.8 (4.7-14.0
Tweedsmuir (R10252)	3,354	Moderate	12	23.6 21.3-28.9	32.2 (29.0-36.0)	23.5 (16.8-28.8)	8.6 (5.5-14.2)
	2013/09/12-2013/09/16	Extreme	0	NA	NA	NA	NA
Chelaslie (R10070)	133,100	Moderate	26	22.3 (3.0-28.7)	38.6 (19.8-68.6)	22.6 (6.2-29.8)	6.5 (1.2-18.3)
	2014/07/09-2014/10/26	Extreme	10	34.6 (29.6-48.3)	27.5 (20.2-43.0)	23.5 (14.1-30.2)	8.9 (1.8-21.4)

Table 2.S2. Estimates for stand structure grouped by cause of death for plots across all three fires that burned through gray-phase outbreak conditions. The estimates include basal area, stem density, quadratic mean diameter (QMD), and percent of lodgepole pine. Estimates are included for pre-outbreak, MPB-killed outbreak severity, prefire-killed mortality, fire-killed mortality, and cumulative mortality disturbance of prefire-killed + fire-killed.

	Stand Structure	Mean	SD	Range
Pre-outbreak	Live Basal Area (m2/ha)	24.6	11.5	5.1-58.5
	Live Stem Density (stems/ha)	1497	755	200-4200
	QMD (cm)	14.9	3.3	9.9-23
	Percent Lodgepole pine (%)	95.9	9.0	63.6-100
MPB-killed Mortality	Basal Area (m2/ha)	17.8	12.2	0-55.3
	Stem Density (stems/ha)	889	571	0-2200
	QMD (cm)	14.0	6.2	0-23
	Percent Lodgepole pine (%)	62.8	32.7	0-100
Prefire-killed Mortality	Basal Area (m2/ha)	18.9	11.4	0-55.3
	Stem Density (stems/ha)	994	520	0-2400
	QMD (cm)	15.1	4.4	0-23.0
	Percent Lodgepole pine (%)	70.0	25.5	0-100
Fire-killed Mortality	Basal Area (m2/ha)	4.9	4.7	0-23.3
	Stem Density (stems/ha)	433	523	0-2800
	QMD (cm)	10.2	5.8	0-18.3
	Percent Lodgepole pine (%)	22.6	23.6	0-100
Cumulative Mortality	Basal Area (m2/ha)	23.8	11.0	5.1-55.3
	Stem Density (stems/ha)	1427	704	200-3900
	QMD (cm)	15.0	3.3	9.9-23.0
	Percent Lodgepole pine (%)	92.6	11.3	59.3-100

Table 2.S3. The relationship between plot-level fire effects metrics and MPB outbreak severity (proportion of MPB-killed trees) under moderate and extreme burning conditions. See Figure 2.2 for a visual of the estimate relationship from the statistical models.

Response variable				95% CI	
Explanatory variable	Estimate	Test statistic	p-value	Lower	Upper
Measured on trees					
Proportion of trees with deep char[†]					
MPB-killed trees: moderate	0.949	$z_{58} = 4.91$	< **0.001**	0.853	0.984
MPB-killed trees: extreme	0.767	$z_{58} = 1.74$	0.141	0.402	0.941
Interaction term [‡]		$\chi^2_1 = 2.85$	0.092		
Proportion of trees with deep char[†]					
Prefire-killed trees: moderate	0.99	$z_{58} = 5.02$	< **0.001**	0.957	0.999
Prefire-killed trees: extreme	0.99	$z_{58} = 7.8$	< **0.001**	0.977	0.998
Interaction term[‡]		$\chi^2_1 = 0.01$	0.92		
Scorch height (m) [§]					
MPB-killed trees: moderate	1.207	$t_{59} = 0.66$	0.508	-2.422	4.836
MPB-killed trees: extreme	-3.705	$t_{59} = -1.30$	0.198	-9.399	1.990
Interaction term[‡]		$F_{3,59} = 2.12$	0.151		
Unscorched area (average proportion)[¶]					
MPB-killed trees: moderate	1.144	$t_{59} = 0.33$	0.740	0.518	2.525
MPB-killed trees: extreme	3.004	$t_{59} = 1.72$	0.090	0.859	10.512
Interaction term[‡]		$\chi^2_1 = 0.75$	0.237		
Measured at the surface					
Remaining litter + duff depth (mm) [§]					
MPB-killed trees: moderate	3.417	$t_{59} = 1.322$	0.191	-1.754	13.373
MPB-killed trees: extreme	5.261	$t_{59} = 1.298$	0.199	-2.852	8.587
Interaction term[‡]		$F_{3,59} = 0.147$	0.703		
Proportion of surface char[#]					
MPB-killed trees: moderate	0.537	$t_{59} = 0.312$	0.756	0.309	0.751
MPB-killed trees: extreme	0.506	$t_{59} = 0.032$	0.975	0.186	0.821
Interaction term[‡]		$\chi^2_1 = 0.0198$	0.889		
Proportion of remaining litter[¶]					
MPB-killed trees: moderate	1.284	$t_{59} = 0.541$	0.590	0.519	3.174
MPB-killed trees: extreme	0.983	$t_{59} = -0.024$	0.981	0.254	3.806
Interaction term[‡]		$\chi^2_1 = 2.85$	0.770		
Proportion of exposed mineral soil[¶]					
MPB-killed trees: moderate	0.862	$t_{59} = -0.285$	0.7766	0.311	2.391
MPB-killed trees: extreme	0.392	$t_{59} = -1.064$	0.292	0.070	2.202
Interaction term[‡]		$\chi^2_1 = 0.422$	0.422		

[†] Response variables were fit to a beta-binomial distribution with a logit link. Estimates and confidence intervals are reported as probabilities.

[‡] Drop-in deviance test for the statistical interaction between the proportion of MPB-killed trees and burning conditions.
[§] Response variable was fit to a normal distribution with estimate and confidence interval reported as means.
[¶] Response variables were fit to a Tweedie distribution using the log link with estimates reported as medians and confidence intervals reported on the multiplicative scale.
[#] Response variable was logit transformed; estimates reported as medians and confidence interval reported on the multiplicative scale.

Table 2.S4. The probability of branch structure loss and deep char development as a function of a tree's cause of death. The odds ratios represent the difference between the probabilities of the response variable when we compare mortality agents (i.e. MPB-killed compared to fire-killed) indicating the magnitude of effect of mortality status on biomass consumption. Results are reported with 95% confidence intervals (CI), Lower Confidence Interval (LCI) and Upper Confidence Interval (UCI). The test statistic for the drop-in-deviance test for statistical significance of the interaction term (i.e., mortality × burning conditions) is reported as chi-squared. The odds ratios were calculated from the odds of group1 divided by the odds of group2, where group1 and group 2 are the odds calculated as (probability/(1-probability)). A large odds ratio indicates a large difference in the probabilities of group 1 compared to group 2. Estimates are illustrated in Figure 2.3.

		95% CI		Odds ratio	95% CI			
Response variable	Probability	LCI	UCI		LCI	UCI	p-value	Test statistic
Loss of branch structure								
MPB-killed (moderate)	0.701	0.397	0.893	8099	267	245460	<0.0001	
Fire-killed (moderate)	0.0003	0.00001	0.006					
MPB-killed (extreme)	0.192	0.042	0.562	94	5	1724	0.0027	
Fire-killed (extreme)	0.003	0.0001	0.045					
Interaction term							0.02935	$\chi^2 = 7.057$
Prefire-killed (moderate)	0.710	0.394	0.902	10297	428	247951	<0.0001	
Fire-killed (moderate)	0.0002	0.00001	0.005					
Prefire-killed (extreme)	0.24	0.051	0.645	246	15	3889	0.0001	
Fire-killed (extreme)	0.0013	0.00005	0.027					
Interaction term							0.05719	$\chi^2 = 3.617$
Deep Char								
MPB-killed (moderate)	0.992	0.968	0.998	9755	776	122564	<0.0001	
Fire-killed (moderate)	0.012	0.003	0.492					
MPB-killed (extreme)	0.976	0.890	0.995	594	37	9531	<0.0001	

Fire-killed (extreme)	0.065	0.010	0.314					
Interaction term							0.1035	χ2 = 4.536
Prefire-killed (moderate)	0.985	0.953	0.996	4106	647	26079	<0.0001	
Fire-killed (moderate)	0.016	0.004	0.057					
Prefire-killed (extreme)	0.968	0.881	0.992	367	49	2772	<0.0001	
Fire-killed (extreme)	0.076	0.015	0.315					
Interaction term							0.04078	χ2 = 4.185

Table 2.S5. The probability of branch structure loss as a function of the amount of coverage of deep char on the tree. Results are reported as probabilities and odds ratios with 95% confidence intervals (CI), Lower Confidence Interval (LCI) and Upper Confidence Interval (UCI). We also report the test statistic, as chi-squared, for the drop-in-deviance test, which tested the statistical significance of the interaction term (i.e., mortality × burning conditions). Estimates are illustrated in Figure 2.5.

		95% CI			
Response Variable	Probability	LCI	UCI	p-value	Test statistic
Loss of Branch structure					
None (moderate)	0.01	0.003	0.03	<0.0001	
< 50% Deep Char (moderate)	0.159	0.085	0.276	<0.0001	
50-100% Deep Char (moderate)	0.931	0.859	0.968	<0.0001	
None (extreme)	0.011	0.001	0.106	<0.0001	
< 50% Deep Char (extreme)	0.108	0.047	0.229	<0.0001	
50-100% Deep Char (extreme)	0.917	0.746	0.977	0.0016	
Interaction term				0.904	$\chi^2 = 0.202$
		95% CI			
Loss of Branch structure	Odds Ratio	LCI	UCI	p-value	
<50% / None (moderate)	18.38	4.98	67.88	<0.0001	
50-100% / None (moderate)	1314.38	306.58	5634.97	<0.0001	
50-100% / <50% (moderate)	71.51	25.49	200.64	<0.0001	
<50% / None (extreme)	11.00	1.02	118.65	0.0957	
50-100% / None (extreme)	1004.35	70.62	14283.88	<0.0001	
50-100% / <50% (extreme)	91.32	19.45	428.61	<0.0001	

CHAPTER 3: Drivers of lodgepole pine recruitment across a gradient of bark beetle outbreaks and wildfire in British Columbia

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Highlights:

- Recruitment was six times greater in burned plots compared to fire refugia
- Cone abundance, as a seed source, was a primary driver of recruitment
- In fire refugia, recruitment post-outbreak was three times greater than pre-outbreak
- The unevenness in recruitment contributes to landscape heterogeneity

Keywords – resilience, serotiny, mountain pine beetle, fire refugia, seedlings

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Abstract

Seedbanks are essential for forest resilience, and disturbance interactions could potentially modify seedbank availability, subsequent forest regeneration patterns, and successional trajectories. Regional mountain pine beetle outbreaks have altered forest structure and seedbanks in fire prone-landscapes across western North America that could influence forest regeneration. We examined the drivers of lodgepole pine recruitment across a gradient of fire severity that burned through gray-phase outbreak conditions in central interior British Columbia, Canada. We considered ten potential drivers of lodgepole pine recruitment including: fire severity, MPB outbreak severity, cone abundance, branch retention, open cones, exposed soil, snag fall, snow accumulation, climate moisture deficit, and frost events, as well as the contribution of unburned fire refugia to lodgepole pine recruitment. In 2016, we inventoried 83 plots that spanned gradients of outbreak severity, burning conditions, and fire severity across three fires that burned through lodgepole pine dominated forests with gray-phase conditions that had moderate to high mortality. We used generalized linear models to evaluate drivers of variability in seedling recruitment. Our analyses affirm that wildfire is a critical mechanism for lodgepole pine seedling recruitment. For plots that burned as crown and surface fire, recruitment densities were two or six times greater compared plots that experienced light surface or were fire refugia, respectively. Recruitment was driven by cone abundance indicating the importance of an available seed source. In fire refugia, recruitment was three times greater during the post-outbreak period compared to before outbreak, which we attributed to cone senescence from mortality and/or xeriscent-cueing of cones. The unevenness in recruitment across gradients of outbreak and wildfire severity contribute to the heterogeneity of stand initiation across these landscapes that may be relevant for mediation of subsequent outbreaks.

Introduction

Landscape-scale disturbances such as mountain pine beetle (*Dendroctonous ponderosae*; hereafter MPB) outbreaks and wildfire are ecological agents that shape composition and structure in the forests across western North America. Insect outbreaks and wildfire are increasing in magnitude under contemporary climate conditions (Dale et al. 2001, Gonzalez et al. 2010), and overlapping in time and space to create conditions with narrow windows between disturbances – i.e. short-interval disturbances (Turner 2010, Buma and Wessman 2011, Harvey et al. 2014b, Edwards et al. 2015). In British Columbia (BC), Canada, the extent of the recent MPB outbreaks in the sub-boreal region, circa 1999-present, has exceeded the magnitude and contiguity of mortality conditions in the western United States (US) over recent decades (Raffa et al. 2008) and in the historical record for BC (Axelson et al. 2009, Perrakis et al. 2014). When fire occurs in these forests, there is concern there could be synergistic interactions between fire and the legacy left by the MPB outbreaks that will influence postfire structural legacies, ecological response, and forest resilience (Talucci and Krawchuk 2019., Holling 1973, Paine et al. 1998, Simard et al. 2011, Johnstone et al. 2016).

Life history traits and seedbank characteristics of trees are key mechanisms influencing forest regeneration and succession following broad-scale disturbances. Lodgepole pine (*Pinus contorta* var. *latifolia*; hereafter lodgepole pine) is a widespread species across western North American forests that exhibits cone serotiny, the retention of an aerial seedbank within sealed cones past maturation and awaiting an environmental cue (Lamont et al. 1991). Serotiny is a key mechanism facilitating postfire regeneration (Lotan et al. 1985, Muir and Lotan 1985, Tinker et al. 1994) and development of early seral stages of forest communities. Seed release from serotinous lodgepole pine tends to be pyriscent (fire cued), but can also be xeriscent – i.e.

opening cued from warm, dry conditions (Lamont et al. 1991), or cone opening triggered by senescence associated with tree mortality (Teste et al. 2011). Pyriscent cones generally trigger a large pulsed seed release, while xeriscent cones tend to trigger seed release from a few cones that experience direct sunlight and is distributed over time (Crossley 1956, Teste et al. 2011). Postfire seedling density is largely controlled by prefire serotiny levels in lodgepole pine (Lotan 1976, Muir and Lotan 1985, Tinker et al. 1994, Turner et al. 1997, Schoennagel et al. 2003); however, severe MPB outbreaks prior to fire may alter typical serotiny responses. Once snags (standing dead trees) drop their needles and transition to what is referred to as the gray-phase of an outbreak (Hopkins 1909, Wulder et al. 2006, Simard et al. 2011), cones may experience additional exposure to direct sunlight that triggers xeriscent cone opening. Even with seed release from a xeriscent cue or live trees with non-serotinous cones, regeneration is slow due to resource competition experienced by seedlings and saplings of these shade-intolerant pines (Astrup et al. 2008, de Ville 2013). By the time MPB-killed snags reach the gray-phase, they are estimated to experience a 45% reduction in the aerial seedbank from xeriscent cone opening, squirrel predation of canopy cones, and relocation of cones from the canopy to the forest floor through branch breakage – i.e. stand “breakdown” (Teste et al. 2011). Snag fall can further contribute to stand breakdown by relocating the entire canopy and seedbank to the surface (Lewis and Hartley 2005). If MPB outbreaks modify the typical serotiny response to subsequent fire (Teste et al. 2011), there is potential for interruption of the usual cueing and postfire regeneration response, creating compound disturbance effects *sensu* Paine et al. (1998).

Wildfire is an important mechanism for seed release from serotinous cones in forests affected by MPB outbreaks; however, the timing is critical and dependent on cone location. When forests experience high outbreak mortality (80-100%; high severity), trees become vulnerable to stand breakdown through branch breakage and wind-throw (Lewis and Hartley 2005), both of which relocate the aerial seedbank to the forest floor. During wildfire, the rate of spread for the initial flaming front is slower at the surface compared to active crown fire, which can expose cones on the forest floor to longer flame residence time that results in ignition, combustion, and extended heating that reduces the seedbank (Alexander and Cruz 2012). Trees that existed as snags before the fire are more likely to torch and smolder, resulting in consumption of bark, branch structure (and accompanying loss of aerial seedbank, either consumed or relocated to the forest floor), and deep char development (Talucci and Krawchuk 2019, Donato et al. 2009). The aggregation of these disturbance effects could result in areas that fail to regenerate. For example, subalpine forest experiencing moderate- to high-severity wind-throw events followed by moderate- to high-severity wildfire failed to regenerate because the aerial seedbank was exposed to slower moving surface fire; however, less severe disturbance conditions from both wind-throw and fire exhibited strong regeneration (Buma and Wessman 2011). These outcomes suggest that synergistic interactions are dependent on the magnitudes of the disturbances that interact. When wildfire burns through stands dominated by lodgepole pine with high mortality from MPB outbreaks and breakdown in snag structure, as seen in BC’s central interior lodgepole pine ecosystems, it is not clear whether these stands will be resilient – i.e., demonstrate the early seral seedling recruitment expected from their pyriscent life history strategy – or whether they may fail to regenerate.

Climate conditions, including winter frost events, snow accumulation, and growing season water stress, are known controls of seedling recruitment. In subalpine environments during colder months, frost events can desiccate seedlings (Stuart et al. 1989, Inouye 2000), while snow accumulation insulates seedlings and provides moisture, thus enhancing survival rates (Batllori et al. 2009, Renard et al. 2016). During warmer months, longer growing periods and warmer conditions boost regeneration capacity, in subalpine environments (Clark et al. 2017). However, extended periods of water stress and/or prolonged drought postfire are suggested to preclude and/or delay regeneration (e.g. Harvey et al. 2016, Hansen et al. 2018). Few studies have examined the relationship between climate and postfire seedling recruitment in BC's sub-boreal forests (Wong et al. 2004). Given the general life zone equivalence of subalpine and sub-boreal systems (Holdridge 1947), recruitment response in the sub-boreal is likely to be influenced by similar variables related to climate and moisture conditions as observed in the subalpine. Characterizing postfire climate is necessary for understanding heterogeneity in early seral forest development.

Previous research investigating lodgepole pine recruitment after MPB outbreak and subsequent wildfire has been concentrated in the US Northern Rocky Mountains (Harvey et al. 2014a, 2014b). These studies consisted of subalpine mixed conifer forests that experienced both lower magnitude and contiguity of prefire tree mortality from MPB when compared to conditions in central interior BC. In these mixed conifer forests, lodgepole pine regeneration postfire was attributed to the proportion of trees that exhibited prefire cone serotiny and was considered unaffected by the MPB outbreak (Harvey et al. 2014a, 2014b). However, the nuances of stand breakdown in forests affected by MPB outbreaks and fire were not explicitly examined, including variability in branch retention and cone abundance. In particular, prior work was unable to parse out the drivers of low tree regeneration observed after wildfire burned through gray-phase conditions (Harvey et al. 2014a), and did not examine the effect of increasing snag fall that occurs later in the gray-phase (Harvey et al. 2014b). The effects of postfire climate were not explicitly tested in previous work, but postfire drought was considered to hinder recruitment

(Harvey et al. 2014a, 2014b). Additionally, previous research has not examined recruitment in MPB-affected fire refugia (Meddens et al. 2018), locations that experience insect outbreak but did not burn within a given fire event, as a contributor of landscape heterogeneity. With multiple landscapes experiencing overlaps of disturbance mosaics across western North America, addressing these research gaps in the BC context may inform future decision-making processes for research and forest ecosystem management.

Here we examine the drivers of lodgepole pine recruitment in early seral forests in central interior BC across a gradient of fire severity generated from burning in gray-phase outbreak conditions. We focus on two objectives. First, we determine the drivers of seedling recruitment across a gradient of fire severity by considering the effect of ten potential contributing factors: fire severity, outbreak severity, cone abundance, branch retention, open cones, exposed soil, snag fall, frost events, snow accumulation, and climate moisture deficit, for areas that experienced MPB outbreak then wildfire. Second, we determine the drivers of seedling establishment in fire refugia, within fire perimeters but only affected by MPB outbreaks, including establishment periods, outbreak severity, cone abundance, branch retention, and open cones. We expected fire to serve as a critical mechanism for seed release and enhanced recruitment across a gradient of fire severity. However, we hypothesized that factors associated with stand breakdown – outbreak severity, cone abundance, branch retention, open cones, and snag fall would act as mechanism that reduce the seedbank between outbreak and wildfire resulting in reduced post-fire recruitment. Factors associated with resource availability on the forest floor, mainly exposed soil, was thought to be a vital mechanism for germination and recruitment that would enhance recruitment and success. Factors associated with postfire climate including snow accumulation, frost events, and climate moisture deficit were hypothesized to either enhance or constrain recruitment depending on the conditions.

Methods

Study Area

Our study area included three wildfire footprints that burned in 2012, 2013, and 2014 within Tweedsmuir and Entiako provincial parks (Figure 3.1). These fires burned through forests with substantial prefire mortality from MPB outbreaks. Lodgepole pine forests experienced severe tree mortality about 10-12 years prior from regional MPB outbreaks, which altered the arrangement of live and dead vegetation/fuels across the landscape. These forests are associated with the Sub-Boreal Pine Spruce and Sub-Boreal Spruce biogeoclimatic zones (Meidinger and Pojar 1991). For the region, Temperatures and precipitation are calculated from the monthly means from the 1981-2010 Climate Normals data (Abatzoglou et al. 2018). The mean maximum temperature is 8.5℃ (range: -3.3-19.8℃), and the mean nighttime temperature is -2.8℃ (range: -11.9-6.7℃). Annual precipitation totals 507.6 mm, and mean monthly precipitation is 42.3mm (range: 22.7-60.8mm) with snowfall during winters months. Forest composition and structure is dictated by moisture gradients and disturbance history (Delong 1998). Pure lodgepole pine stands occupy the driest portions of the moisture gradient and persists with estimated fire return intervals of 100-150 years (Parminter 1992), seral lodgepole pine communities with subalpine fir (*Abies lasiocarpa*) and spruce hybrid (*Picea engelmannii* x *glauca*) that persist when fire return intervals that are longer, and the wettest pockets dominated by spruce, such as riparian zones or moist areas with long periods without fire (Cichowski and Morgan 2009). The landscape is gently rolling with elevation ranging from 873m to 1057m.

The study area has no road access, and sampling was limited within 10 km radius hiking and boating distances from three remote cabins in the provincial parks. The parks are managed as wilderness and provided an ideal setting to study MPB-fire interactions without the influence of active forest management (e.g. harvest, suppression). All fires received minimal to no suppression activities (Rob Krause and Mike Pritchard, BC Wildfire Service, *personal communication*). The Entiako Lake fire was lightning ignited on August 3 2012, and burned until September 22 2012, burning 7,450 ha (BCWS 2016). The Tweedsmuir fire was lightning ignited on September 9 2013, and burned until September 16 2013, burning 3,600 ha (BCWS 2016). The Chelaslie River fire was lightning ignited on July 8, 2014, and burned until October 26 2014, burning 133,100 ha (BCWS 2016).

Sampling Design and Data

We conducted field sampling from June through August 2016. Data collection captured various stages of development for early successional forest communities from two to four years postfire. Sampling captured a gradient of fire severity and outbreak severity including fire refugia that only experienced MPB outbreak. We conducted an initial *a priori* site selection using digital data that included aerial survey maps of outbreak severity (BCMFLNRO 2016), burn severity maps developed following methods developed by Eidenshink et al. (2007), and vegetation maps based on the Vegetation Resource Inventory, a provincial inventory generated from aerial photos (BCMFLNRO 2012). Plots were distributed across a gradient of MPB outbreak severity and fire severity while targeting areas with over 75% lodgepole pine in the canopy based on vegetation maps. We conducted a final visual assessment on the ground to ensure plots were representative of the surrounding area and that lodgepole pine was the primary canopy tree species.

In the field, we navigated to pre-selected plot locations and, if they met the *a priori* design criteria, selected plot center to ensure a representative sample of the area. UTM coordinates were recorded at the plot center with a Global Positioning System (GPS; Garmin GPSMAP 78s). Each plot measured ten-by-ten-meter (100 m^2; 0.01 ha). We divided each plot into four quadrants along the north-south and east-west axes identified as NE, SE, SW, and NW. Within each quadrant a one-by-one-meter (1 m^2) subplot was situated at increasing distances from the center of the plot (NE-1m, SE-2m, SW-3m, and NW-4m) and used to measure tree recruitment and surface fire effects, described below. We surveyed all canopy trees in each plot, including live trees, snags, and fallen snags (i.e. coarse woody debris) that would have been canopy trees prior to falling. For each canopy tree, we recorded the species, whether it was alive or dead at time of sampling, the diameter at breast height to the nearest 0.5 cm, evidence of beetle activity, variables associated with stand breakdown, and first-order fire effects as measures of fire severity.

For each canopy tree, we identified the cause of death (i.e., MPB, fire, or other; Appendix Table 3.S1) following protocols outlined by Talucci and Krawchuk (2019) and adapted from Harvey et al. (2013, 2014a). Dead trees identified as MPB-killed had evidence of exit holes and j-shaped galleries specific to MPB. Trees classified as “other-killed” lacked evidence of exit holes and j-shaped galleries specific to MPB, however other evidence indicated prefire mortality including Ips beetle (*Ips pini*) activity, needle loss, sloughing bark, and decay and/or deep char at the base. A tree was classified as fire-killed if it exhibited red needles in the canopy or postfire needle drop and no evidence of prefire MPB or other beetle activity. Most of the prefire tree mortality present was linked to MPB (Appx. Table 3.S1). At the plot-level, outbreak severity was represented as the proportion of prefire-killed trees, which was the combination of MPB-killed plus other-killed trees (Appx. Table 3.S1).

We characterized metrics of stand breakdown – outbreak severity (described above), branch retention, open cones, cone abundance, and snag fall. Branch retention was characterized as the presence or absence of fine, moderate, and coarse branch structure in the canopy. Absence indicated no remaining branch structure on either the tree or the ground in the immediate area of the tree meaning that branches were consumed by fire. Presence denoted at least partial to full branch structure on a tree. Branch retention was aggregated to a plot-level variable as the proportion of trees with branches. Each tree was classified according to whether it had a majority of cones open, scored as one for yes and zero for no, and then calculated as proportion of trees with open cones per plot. We counted cones retained in the tree canopy using binoculars and a tally counter, to serve as a general estimate of potential seed availability. We calculated a plot-level variable of cone abundance as the mean cones per tree. Our snag fall metric accounted for all prefire snag fall, which was consider a component of stand breakdown that could influence seedbank availability. Prefire snag fall was distinguished from postfire snag fall based on presence of charring at the break point of the snag and was absence on postfire snags. We calculated a plot-level metric of the proportion of prefire snag fall indicating re-location of seedbank to the surface prior to fire.

We characterized fire severity using nine fire effects metrics including scorch/char height on trees, percentage of scorch/char on stem, level of deep char, depth of remaining litter/duff, exposed mineral soil, remaining litter, and terrestrial surface char. Because plots were surveyed between two to four years postfire, they captured various early successional stages of postfire litter accumulation and vegetative regrowth. We estimated the height of maximum bark scorch/char to the nearest 0.5 m with a four-meter measuring stick. We visually estimated and recorded the percentage of the tree covered with scorch/char across the height and circumference and assigned a category for the percentage of deep charring on the full height and circumference of the tree (0 percent, < 50 percent, or ≥ 50 percent). Within each subplot, we quantified and recorded surface fire effects metrics including duff depth, exposed mineral soil, remaining litter, and surface char based on a visual estimate of the percent cover. We measured the combined litter and duff depth to the nearest millimeter with a ruler in two opposing corners of each subplot. The proportion of exposed mineral soil was considered a contributing factor for seedling recruitment in our analyses. In the field, we assigned each plot a fire severity class: unburned, light surface, severe surface, or crown fire based on visual inspection of fire effects. Each fire effect was aggregated to a plot-level metric. We evaluated our fire severity classes with scatter plots and a classification tree using our plot-level fire effects to confirm their validity and retained those classes for analysis (Appx. Figure 3.S1).

We represented postfire climate as annual frost-free days, annual snow accumulation, and annual climate moisture deficit, acquired from the Climate BC dataset (Hamann and Wang 2018). We downloaded monthly climate variables from 2012 to 2015 and calculated an annual value for each variable at each plot based on the postfire year, October through September of the year following each fire. We proposed higher snow accumulation would insulate and protect seedlings during cold winter months, which would enhance recruitment success, while increased exposure to frost events could result in seedling mortality due to freezing. We expected recruitment to decline if climate moisture deficits were greater due to the stress and mortality associated with reduced moisture availability during the growing season.

We recorded seedlings and saplings (recruits) in burned and unburned plots. In burned plots, we recorded counts of all recruits in the one-by-one-meter subplots, as well as seedlings in two of the four 5-by-5-meter quadrants. This nested strategy ensured a representative sample of recruits while maintaining sampling efficiency. For analysis, we aggregated recruitment counts to a plot-level variable. In unburned (fire refugia) plots, we recorded all recruits in the full 10-by-10-meter plot because of the low recruitment density. For each recruit in unburned plots, we recorded the number of branch whorls as a proxy for a general estimate of year of establishment and measured the diameter at the base of each recruit.

Statistical Analysis

We used multiple analyses to address our two research objectives, as outlined in Table 3.1. Due to the relatively small data set, we tested the effect of each factor on seedling counts with an individual analysis (Table 3.1). We used generalized linear models with a negative binomial distribution, using a log link, for all analyses. All models addressing our first objective included an offset variable that accounted for the area in which recruits were counted. To evaluate the effect of fire severity, we tested for a difference in mean number of recruits among our fire severity classes – crown, severe surface, light surface, and fire refugia. To determine the effect of the other contributing factors we regressed the number of recruits against each factor – outbreak severity, branch retention, open cones, cone abundance, soil exposure, frost events, snow accumulation, and climate moisture deficit and included an interaction term with fire severity. For our second objective, we evaluated the potential drivers of recruitment in fire refugia. We tested for a difference in mean number of recruits across establishment periods – pre-outbreak (1990-1998), during outbreak (1999-2006), and post-outbreak (2007-2015) periods.

We then regressed the number of recruits against each potential contributing factor – outbreak severity, branch retention, open cones, and cone abundance. All statistical analyses were conducted in R statistical computing software version 3.4.4 (R Development Team 2018). We assessed model fit for all models through an inspection of the residuals and tested for overdispersion, which was not an issue in any of our models. Results were interpreted based on effect sizes and with p-values that ranged between 0.05 and 0.10. Data and code for analyses are available online (Talucci 2019).

Results

Across the three fires sampled, mature lodgepole pine accounted for 96 percent of the canopy trees surveyed, with spruce accounting for the remaining 4%. We surveyed a total of 1191 trees, with 943 trees in 63 plots that experienced fire and 248 trees within 20 plots in fire refugia (Appx. Table 3.S2). The mean prefire lodgepole pine mortality was 71% (range: 0-100% per plot). Fire caused mortality accounted for an additional 17% (range: 0-100%) for canopy lodgepole pine. Postfire seedling recruitment had a mean density of 12,202 recruits per hectare (range: 0-170,000), which exceeded the mean pre-disturbance canopy tree density of 1,435 (range: 200-4,200) trees per hectare (Appendix Table 3.S2).

Drivers of recruitment across a gradient of fire severity

Across a gradient of fire severity, fire appeared to be a key mechanism and driver of lodgepole pine seedling recruitment. Plots that burned had significantly more recruits than fire refugia (Figure 3.2). In plots that experienced crown fire and severe surface fire, seedling recruitment was over six times greater compared to fire refugia. In plots that experienced light surface fire, seedling recruitment was 2.94 times greater than plots in fire refugia (Figure 3.2).

While accounting for fire severity, variability in seedling recruitment was primarily driven by cone abundance with other stand breakdown variables, soil, and climate variables having limited to no influence (Figure 3.3). Seedling recruitment increased with increasing cone abundance (i.e. mean cones per tree) for plots that experienced severe and light surface fire. Seedling recruitment demonstrated an inverse relationship and declined with increasing cone abundance in plots that experienced crown fire. Seedling recruitment increased in response to the increasing proportion of trees with branches in plots that experienced light surface fire but showed no evidence of a relationship in plots that experienced severe surface and crown fire. All three postfire climate variables – frost events, snow accumulation, and climate moisture deficit, had three prominent outliers that influenced their statistical relationships and significance (Appx. Figure 3.S2). Frost events showed no evidence of a relationship with seedling recruitment with and without outliers. Snow accumulation showed evidence of a direct negative relationship with seedling recruitment with the outliers included, but no evidence of a relationship when outliers were excluded. Climate moisture deficit showed no evidence of a relationship with the number of recruits when outliers were included but showed a decline in seedling recruitment as the climate moisture deficit increased with outliers excluded.

Drivers of recruitment across fire refugia

In fire refugia, recruits showed a pulse after the peak of the MPB outbreaks (Figure 3.4). Recruits had a median age of 10 years (range: 1-27), and a median diameter at their base of 1cm (range: 1-10cm). In the post outbreak period, recruitment was just over three times greater than estimated for the pre-outbreak period (Figure 3.4). Factors associated with stand breakdown – including outbreak severity, proportion of trees with open cones, proportion of trees with branches, and mean cones per tree (i.e. cone abundance), showed no statistical evidence of an effect on the number of recruits (Figure 3.5).

Discussion

Fire is a catalyst for lodgepole pine regeneration in these systems even after 10 years of stand breakdown and cone opening following MPB outbreak. The pulse in postfire recruitment emphasizes the importance of wildfire as a mechanism for seed release and regeneration in these serotinous lodgepole pine forests. Fire severity and cone abundance were the primary drivers of recruitment density in burned stands, while substantial underlying tree mortality from the MPB outbreaks did not play a role. However, cone abundance may be acting as a partial proxy for MPB severity and stand breakdown variables. In fire refugia, a pulse in post outbreak recruitment appeared to contribute to regeneration, but still had substantially lower densities of seedlings and saplings in comparison to their burned counterparts. Patches of the landscape that experience lower recruitment rates may lead to delayed recovery of lodgepole pine that could contribute important structural or demographic heterogeneity to the system (Seidl et al. 2016), but also offer possible foot-holds for slow shifts in composition and structure in response to global change (Stralberg et al. 2018).

Drivers of recruitment across a gradient of fire severity

Wildfire is a key mechanism for seed establishment, with burned plots experiencing higher recruitment rates than fire refugia. Seedling density was highest in plots that experienced severe surface fire, which aligns with previous research that examined beetle-fire interactions in subalpine forests (Harvey et al. 2014a, 2014b). We did not detect a statistical difference in recruitment rates between areas burned by crown and severe surface fires, potentially because crown and severe surface fire produced similar conditions for seed release and site conditions conducive for germination. Serotiny levels are known to be relatively high in the region (DeLong and Kessler 2000). While the canopy seedbank is reduced through relocation to the forest floor from stand breakdown (Teste et al. 2011), lodgepole pine seems to generally produce enough cones and seeds that regeneration is not hindered even when disturbances recur within a short interval.

Stand breakdown following MPB outbreaks can influence the structural and ecological legacies that persist through short-interval MPB-fire interactions that act as controls for regeneration and contribute to the postfire landscape heterogeneity. The proportion of prefire mortality, remaining branch structure, cone abundance, open cones, and snag fall were factors that we hypothesized might influence seedling recruitment postfire and could potentially be correlated. Cone abundance was the only clear driver of recruitment amongst these factors and was not correlated with MPB severity, but it was moderately correlated with remaining canopy structure (r=0.61). In plots that experienced severe and light surface fire, recruitment had a direct positive relationship with cone abundance. However, in plots that experienced crown fire, recruitment declined with increasing cone abundance, which may point to instances where overheating kills seeds (Alexander and Cruz 2012) or other correlating effects that we were unable to tease apart. This finding highlights that serotiny is a key trait for lodgepole pine regeneration even after stand breakdown from MPB outbreaks (Schoennagel et al. 2012, Harvey et al. 2014a, 2014b), while absence of regeneration has been found after fire in regions dominated by non-serotinous lodgepole pine (Agne et al. 2016).

Exposed mineral soil did not systematically influence seedling recruitment in our burned landscapes, even though it is known to be important for lodgepole pine germination and recruitment (Lotan et al. 1985). Increased exposure of mineral soil is often associated with significant canopy mortality, which frees up available resources for seedling regeneration including water, nutrients, and full sun (Lotan et al. 1985). The exposed mineral soil variable was based on a visual estimate of percent coverage and was measured in early successional forest communities two to four years postfire. The true values of this could have been obscured or under-estimated due to vegetative regrowth. We also did not specifically measure microsite characteristics such as soil type, moisture levels, or nutrient levels, which can also influence seedling success and/or failure (Inouye 2000, Batllori et al. 2009, Walck et al. 2011, Harvey et al. 2016, Renard et al. 2016, Clark et al. 2017, Hansen et al. 2018) and should be considered in future research.

Postfire climate conditions are relevant drivers of seedling recruitment and success. Frost events, snow accumulation, and water stress are known to influence seedling success in other subalpine systems (Inouye 2000, Batllori et al. 2009, Walck et al. 2011, Harvey et al. 2016, Renard et al. 2016, Clark et al. 2017, Hansen et al. 2018). Due to the life zone equivalence of subalpine and sub-boreal forests (Holdridge 1947), we expected similar climate controls on seedling response to apply. In the year following each fire, there were fewer frost events, less snow, and a greater climate moisture deficit compared to the climate normals data for 1961-2000 and 1981-2010 in ways that indicated anomalously warm and dry conditions. However, the narrow geographical range of our field sites and limited temporal comparison (e.g., three years for contrast), combined with the coarse resolution of the climate data provided a low range of variability within our data and limited our ability to discern effects. Snow accumulation and climate moisture deficit both indicated some control over seedling recruitment, but this varied with the inclusion or exclusion of prominent outliers. With outliers removed, seedling recruitment declined with increasing climate moisture deficit. This general trend aligns with previous findings that identified drought effects as constraints on postfire recruitment (Harvey et al. 2016, Petrie et al. 2016). Under future conditions, sub-boreal landscapes may begin to experience increased stress as the climate warms, which could limit regeneration (Dale et al. 2001, Flannigan et al. 2009, Gonzalez et al. 2010). The combination of disturbances that recur at short intervals with sequential drought events may open opportunities for range shifts in species distributions and forest composition (Johnstone et al. 2016, Stralberg et al. 2018).

Drivers of recruitment across fire refugia

In fire refugia, we observed a pulse in recruitment after the peak of the outbreak. In the post outbreak (2007-2015) period, recruitment establishment was three times greater than compared to before the outbreak (1990-1998). Recruitment periods covered nearly three decades of establishment. Data collection solely captured recruits that existed at time of sampling and does not account for potential mortality over time. In central interior BC, lodgepole pine is known to have high levels of serotiny (Carlson 2008), and although non-serotinous lodgepole pine exists, it is often associated with lower density, mixed-aged stands (DeLong and Kessler 2000). The timing of recruitment suggests that stands in fire refugia were likely producing serotinous cones that senesced and opened as a function of outbreak-based mortality senescence, based on Teste et al. (2011a) analysis of seed loss and/or xeriscent-cueing. However, the population could also include a chronic level of non-serotinous individuals; our postfire data collection did not specifically aim to quantify levels of serotiny. Gradients in factors associated with stand breakdown – MPB mortality, branch structure, cone opening, and cone abundance – did not show evidence of an effect on seedling recruitment among our fire refugia plots. In the shade of snags and with no exposed mineral soil, recruits appeared relatively stunted and less robust compared to their postfire counterparts, likely due to resource competition and lower light levels as described by Astrup et al. (2008) and consistent with findings by de Ville (2013) in southern interior BC. In this post-MPB landscape, fire refugia augment landscape heterogeneity for the broader mosaic by supporting forest patches with lower density and a mixed age structure of lodgepole pine.

Management Considerations

These findings contribute insight on forest management for both protected areas (e.g., provincial parks, national parks) and lands managed for timber production (public/crown and private lands) that have been impacted by recent MPB outbreaks. Fire is a critical mechanism for seed release and recruitment for lodgepole pine dominated forests that experience severe MPB outbreaks. Fire serves to jump-start and accelerate the regeneration of lodgepole pine dominated landscapes with substantial mortality from outbreaks, which is prudent if/when managing for forest regeneration. Within burn mosaics dominated by high severity fire, the arrangement and size of fire refugia are an important consideration for land management and conservation, because they augment postfire early seral forests with heterogeneous patches where fire effects were minimal or absent. In the landscapes studied here, fire refugia encompassed gradients of composition, structure, and succession including early seral forests developing after mortality from recent mountain pine beetle and mature forests dominated by live trees. These patches of fire refugia can act as micro ecosystems that provide structural and ecological diversity (Meddens et al. 2018) including seed sources (Turner et al. 1997) and habitat for wildlife (Robinson et al. 2013). The unevenness in recruitment across gradients of wildfire and MPB outbreak severity, including fire refugia, contribute to landscape heterogeneity that may mediate future outbreaks and enhance forest resilience.

Conclusions

Sub-boreal lodgepole pine forests are generally resilient when MPB outbreaks and wildfire recur in short intervals, with wildfire serving as a key mechanism for seed release and forest regeneration. The postfire burn mosaic contributes to landscape heterogeneity through variability in stand density and age classes. In BC, the recent fire seasons, 2017 and 2018, have been notable in social costs and wildfire footprints with a record number of evacuees and a historic number of hectares burned. The 2017 and 2018 fire seasons have also burned large portions of central interior BC that include forests impacted by MPB outbreaks. Our results point to the resilience of these forests to burning, however as these forests are regenerating they are potentially vulnerable to future increases in fire activity that could lead to young forests experiencing a reburn event, where fires recur in short intervals. Early seral lodgepole pine forests on these landscapes often will not produce serotinous cones for another couple of decades limiting the seedbank development (Lotan and Perry 1983) and constraining their regeneration capacity (Johnstone et al. 2016). Further evaluation and monitoring of forest regeneration in relation to future disturbance dynamics that may influence forest resilience will enhance the ability to characterize successional trajectories for these landscapes under short-interval disturbance regimes and global change.

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Literature Cited

Abatzoglou, J. T., S. Z. Dobrowski, S. A. Parks, and K. C. Hegewisch. 2018. Terraclimate, a high-resolution global dataset of monthly climate and climate water balance from 1958-2015. Scientific Data.

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

Alexander, M. E., and M. G. Cruz. 2012. Modelling the impacts of surface and crown fire behavior on serotinous cone opening in jack pine and lodgepole pine forests. International Journal of Wildland Fire 21:709–721.

Astrup, R., K. D. Coates, and E. Hall. 2008. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. Forest Ecology and Management 256:1743–1750.

Axelson, J. N., R. I. Alfaro, and B. C. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. Forest Ecology and Management 257:1874–1882.

Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutiérrez. 2009. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. Implications and potential responses to climate warming. Global Ecology and Biogeography 18:460–472.

BCMFLNRO. 2012. Vegetation Resources Inventory. British Columbia Ministry of Forests Lands and Natural Resource Operations, Victoria, BC, Canada.

BCMFLNRO. 2016. Aerial overview survey. https://www2.gov.bc.ca/gov/content/environment/research-monitoring-reporting/monitoring/aerial-overview-surveys/data-files.

BCWS. 2016. Historical fire perimeters. British Columbia Wildfire Service, Victoria, BC.

Buma, B., and C. A. Wessman. 2011. Disturbance interactions can impact resilience mechanisms of forests. Ecosphere 2:1–13.

Carlson, M. 2008. East-west trend of decreasing serotiny, relayed through mountain pine beetle seedling planning.

Cichowski, D., and D. Morgan. 2009. Tweedsmuir-Entiako Caribou Population: Summary of Ecology and Effects of Disturbance. Smithers, BC.

Clark, J. A., R. A. Loehman, and R. E. Keane. 2017. Climate changes and wildfire alter vegetation of Yellowstone National Park, but forest cover persists. Ecosphere 8.

Crossley, D. I. 1956. Effect of crown cover and slash density on the release of seed from slash-borne lodgepole pine cones. Page Forest Research Divsion Technical Note No. 41. Canada.

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

Delong, S. C. 1998. Natural disturbance rate and patch size distribution of forests in northern British Columbia : implications for forest management 72.

DeLong, S. C., and W. B. Kessler. 2000. Ecological characteristics of mature forest remnants by wildfire. Forest Ecology and Management 131:93–106.

Donato, D. C., J. L. Campbell, J. B. Fontaine, and B. E. Law. 2009. Quantifying char in postfire woody detritus inventories. Fire Ecology 5:104–115.

Edwards, M., M. A. Krawchuk, and P. J. Burton. 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire. Forest Ecology and Management 338:163–175.

Eidenshink, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, S. Howard, S. Falls, and S. Falls. 2007. A Project for Monitoring Trends in Burn Severity. Fire Ecology 3:3–21.

Flannigan, M., B. Stocks, M. Turetsky, and M. Wotton. 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. Global Change Biology 15:549–560.

Gonzalez, P., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Global Ecology and Biogeography 19:755–768.

Hamann, A., and T. Wang. 2018. Climate BC/WNA/NA. http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/#ClimateBC.

Hansen, W. D., K. H. Braziunas, W. Rammer, R. Seidl, and M. G. Turner. 2018. It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99:966–977.

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

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecological Applications 24:1608–1625.

Harvey, B. J., D. C. Donato, and Turner. 2016. High and dry: Postfire drought and large stand-replacing burn patches reduce postfire tree regeneration in subalpine forests. Global Ecology and Biogeography 25:655–669.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proceedings of the National Academy of Sciences 111:15120–15125.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367–368.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Hopkins, A. D. 1909. Practical information on the Scolytid beetles of North American forests. Page Barkbeetles of the genus Dendroctonous. Washington, DC.

Inouye, D. W. 2000. The ecological and evolutionary significance of frost in the context of climate change. Ecology Letters 3:457–463.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. W. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Lamont, B. B., D. C. Le Maitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. Botanical Review 57:277–317.

Lewis, K. J., and I. D. Hartley. 2005. Rate of deterioration, degrade and fall of trees killed by mountain pine beetle: a synthesis of the literature and experiential knowledge. Page Mountain Pine Beetle Initiative.

Lotan, J. E. 1976. Cone serotiny - fire relationships in lodgepole pine. Tall Timbers Fire Ecology Conference Proceedings 14:267–278.

Lotan, J. E., J. K. Brown, and L. F. Neuenschwander. 1985. Role of fire in lodgepole pine forests. Pages 133–152 *in* D. Baumgartner, editor. Lodgepole pine the species and its management. Lodgepole pine the species and its management Symposium Proceedings, Washington State University, Pullman.

Lotan, J. E., and D. A. Perry. 1983. Ecology and regeneration of lodgepole pine. U.S. Department of Agriculture, Forest Service, Washington, DC.

Meddens, A. J. H., C. A. Kolden, J. A. Lutz, A. M. S. Smith, C. A. Cansler, J. T. Abatzoglou, G. W. Meigs, W. M. Downing, and M. A. Krawchuk. 2018. Fire refugia: what are they, and why do they matter for global change? BioScience.

Muir, P. S., and J. E. Lotan. 1985. Serotiny and life history of Pinus contorta var. latifolia. Canadian Journal of Botany 63:938–945.

Paine, R. T., M. J. Tegner, and E. a. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1:535–545.

Parminter, J. 1992. Typical historic patterns of wildfire disturbance by biogeoclimatic zone. Minsitry of Forests, Victoria, British Columbia, Canada.

Perrakis, D. D. B., R. a. Lanoville, S. W. Taylor, and D. Hicks. 2014. Modeling wildfire spread in mountain pine beetle-affected forest stands, British Columbia, Canada. Fire Ecology 10:10–35.

Petrie, M. D., A. M. Wildeman, J. B. Bradford, R. M. Hubbard, and W. K. Lauenroth. 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. Forest Ecology and Management 361:328–338.

R Development Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Renard, S. M., E. J. B. Mcintire, and A. Fajardo. 2016. Winter conditions - not summer temperature - influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec. Journal of Vegetation Science 27:29–39.

Robinson, N. M., S. W. J. Leonard, E. G. Ritchie, M. Bassett, E. K. Chia, S. Buckingham, H. Gibb, A. F. Bennett, and M. F. Clarke. 2013. Refuges for fauna in fire-prone landscapes: Their ecological function and importance. Journal of Applied Ecology 50:1321–1329.

Schoennagel, T., M. G. Turner, and W. H. Romme. 2003. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. Ecology 84:2967–2978.

Schoennagel, T., T. T. Veblen, J. F. Negron, and J. M. Smith. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE 7:1–14.

Seidl, R., D. C. Donato, K. F. Raffa, and M. G. Turner. 2016. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. Proceedings of the National Academy of Sciences 113:13075–13080.

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

Stralberg, D., X. Wang, M.-A. Parisien, F.-N. Robinne, P. Sólymos, C. L. Mahon, S. E. Nielsen, and E. M. Bayne. 2018. Wildfire-mediated vegetation change in boreal forests of Alberta, Canada. Ecosphere 9:e02156.

Stuart, J. D., J. K. Agee, and R. I. Gara. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. Canadian Journal of Forest Research 19:1096–1104.

Talucci, A. C., and M. A. Krawchuk. 2019. Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. Ecosphere 10(5):e02744. 10.1002/ecs2.2744

Talucci, A. C. (2019). Data and Code: Recruitment after beetle outbreaks and wildfires (Version v0.1) [Data set]. Zenodo. http://doi.org/10.5281/zenodo.3235807

Teste, F. P., V. J. Lieffers, and S. M. Landhäusser. 2011. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecological Applications 21:150–162.

Tinker, D. B., W. H. Romme, W. W. Hargrove, R. H. Gardner, and M. G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Canadian Journal of Forest Research 24:897–903.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67:411–433.

de Ville, N. 2013. Forest light and structure in relation to disturbances: comparing mountain pine beetle, wildfire, and salvage logging. Simon Fraser University.

Walck, J. L., S. N. Hidayati, K. W. Dixon, K. Thompson, and P. Poschlod. 2011. Climate change and plant regeneration from seed. Global Change Biology 17:2145–2161.

Walton, A. 2012. Provincial-level projection of the current mountain pine beetle outbreak: update of the infestation projection based on the 2010 provincial aerial overview of forest health and the BCMPB model (year 9). British Columbia Forest Service:1–15.

Westfall, J., and T. Ebata. 2014. 2014 Summary of forest health conditions in British Columbia. Victoria, BC.

Wong, C., H. Sandmann, and B. Dorner. 2004. Historical Variability of Natural Disturbances in British Columbia: A Literature Review.

Wulder, M. a., C. C. Dymond, J. C. White, D. G. Leckie, and A. L. Carroll. 2006. Surveying mountain pine beetle damage of forests: A review of remote sensing opportunities. Forest Ecology and Management 221:27–41.

Tables

Table 3.1. Study objectives, explanatory variables, and description of explanatory variables to evaluated drivers of seedling recruitment across a gradient of fire severity and in fire refugia. Due to our small sample size, we conducted multiple analyses to evaluate potential drivers of seedling recruitment. Sample sizes for each analysis are indicated in parentheses. Note that explanatory variable 1 × explanatory variable 2 indicates the inclusion of an interaction term, while explanatory variable 1 + explanatory variable 2 does not include an interaction term. All terms in the models were treated as fixed effects.

Explanatory variables	Description of explanatory variable
Objective 1: determine the drivers of seedling recruitment across gradient of fire severity	
Fire severity	Categorical variable including crown, severe surface, light surface, and unburned (n=83)
Outbreak severity × fire severity	Outbreak severity is continuous proportion of prefire-killed trees (n=63)
Branch retention × fire severity	Proportion of trees with remaining branch structure (n=63)
Open cones × fire severity	Proportion of trees with open cones (n=63)
Cone abundance × fire severity	Mean cones per tree/snag (n=63)
Exposed soil × fire severity	Proportion of estimate exposed mineral soil for a plot (n=63)
Snag fall × fire severity	Proportion of prefire snag fall (n=63)
Frost events × fire severity	Total frost-free days one year after fire, calculated from October through September (n=63)
Snow accumulation × fire severity	Total precipitation as snow one year after fire, calculated from October through September (n=63)
CMD × fire severity	Total climate moisture deficit (CMD) one year after fire, calculated from October through September (n=63)
Objective 2: determine the drivers of seedling establishment in fire refugia, areas only affect by MPB outbreaks	
Establishment periods	Categorical variable that divided seedlings into establishment periods based on estimated age, which included pre-outbreak (1990-1998), during outbreak (1999-2006), and post outbreak (2007-2015). (552 saplings across n=20 plots)
Outbreak severity	Proportion of prefire-killed trees (n=20)
Outbreak severity + branch retention	Proportion of trees with remaining branch structure (n=20)
Outbreak severity + open cones	Proportion of trees with open cones (n=20)
Outbreak severity + cone abundance	Mean cones per tree/snag (n=20)

Figures

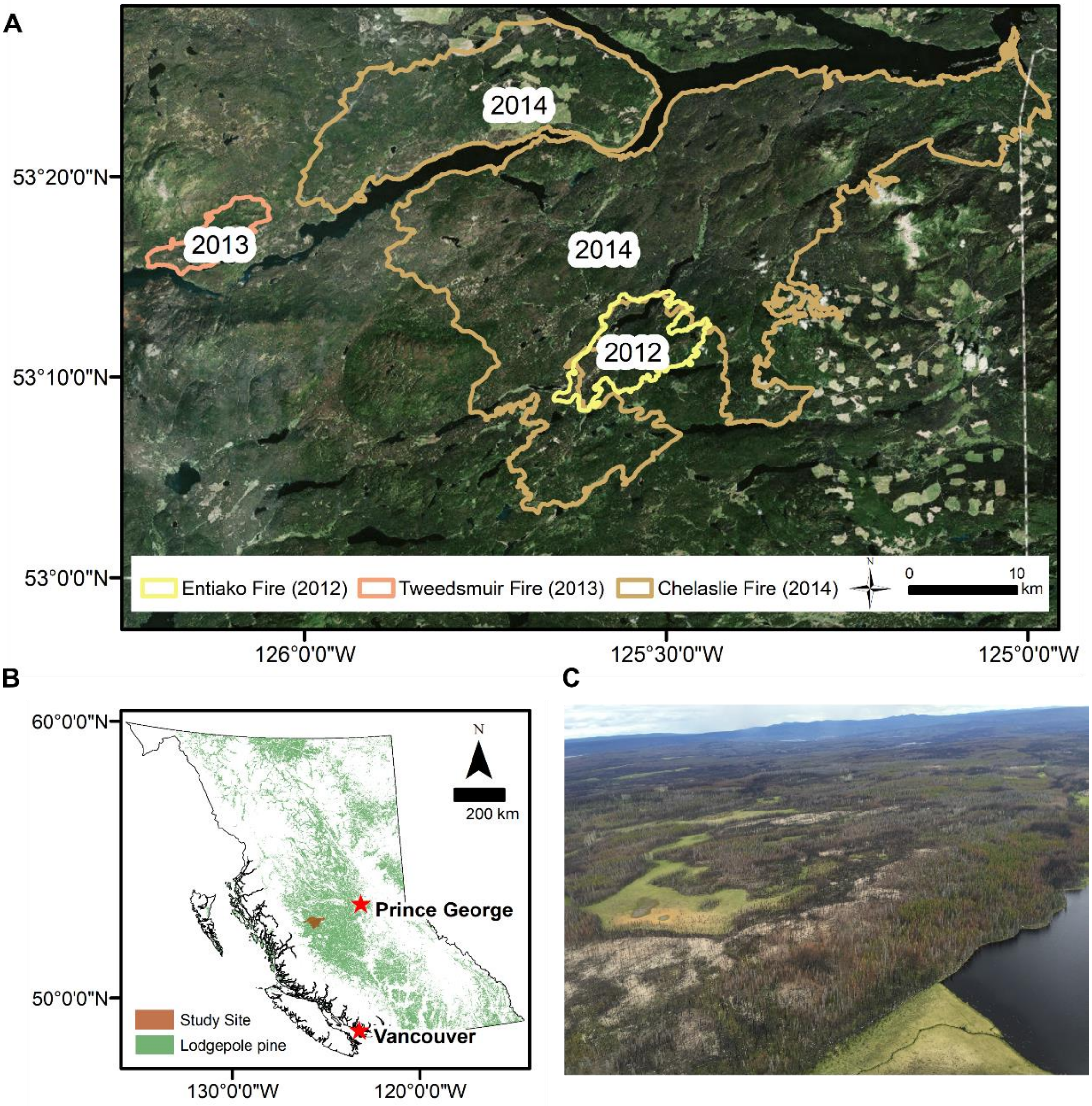

Figure 3.1. Geography of the study area. (A) Fire perimeters for three study fires that burned in 2012 (Entiako Fire; 7,459 ha), 2013 (Tweedsmuir Fire; 3,354 ha), and 2014 (Chelaslie Fire; 133,000 ha). (B) Location of study area and the distribution of lodgepole pine within British Columbia, Canada. (C) Aerial photograph of postfire landscape at Chelaslie River.

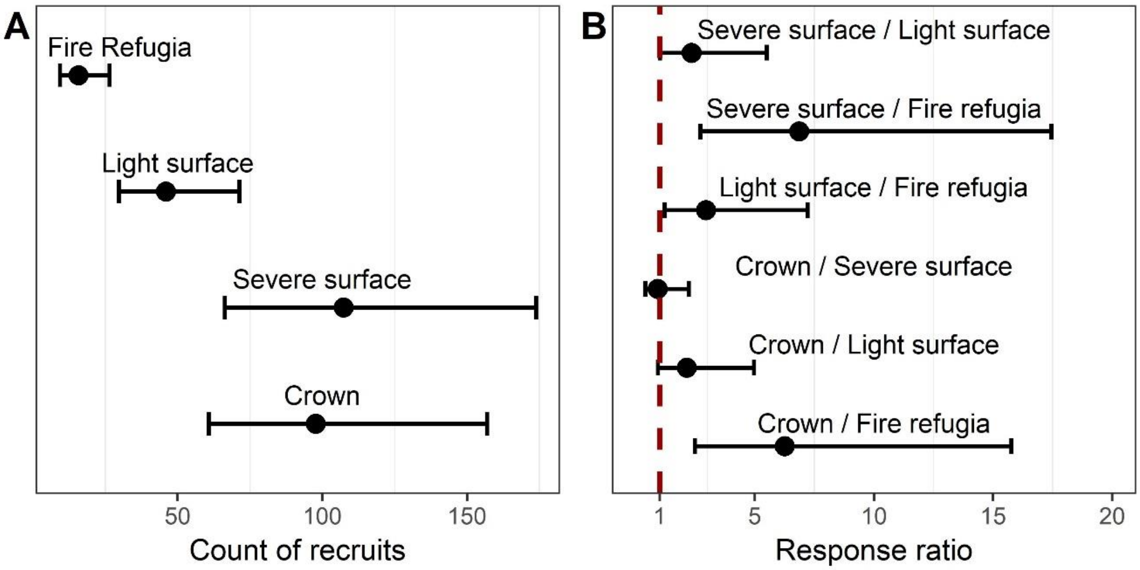

Figure 3.2. Seedling recruitment across a gradient of fire severity. Estimated mean seedling counts per plot by fire severity classifications are shown in **A** with estimated 95% confidence intervals. The difference between fire severity classes is shown in **B** with 95% confidence intervals with a red dashed line at one, which indicates no difference between the groups. Model estimates and response ratios are listed in Appx. Table 3.S3.

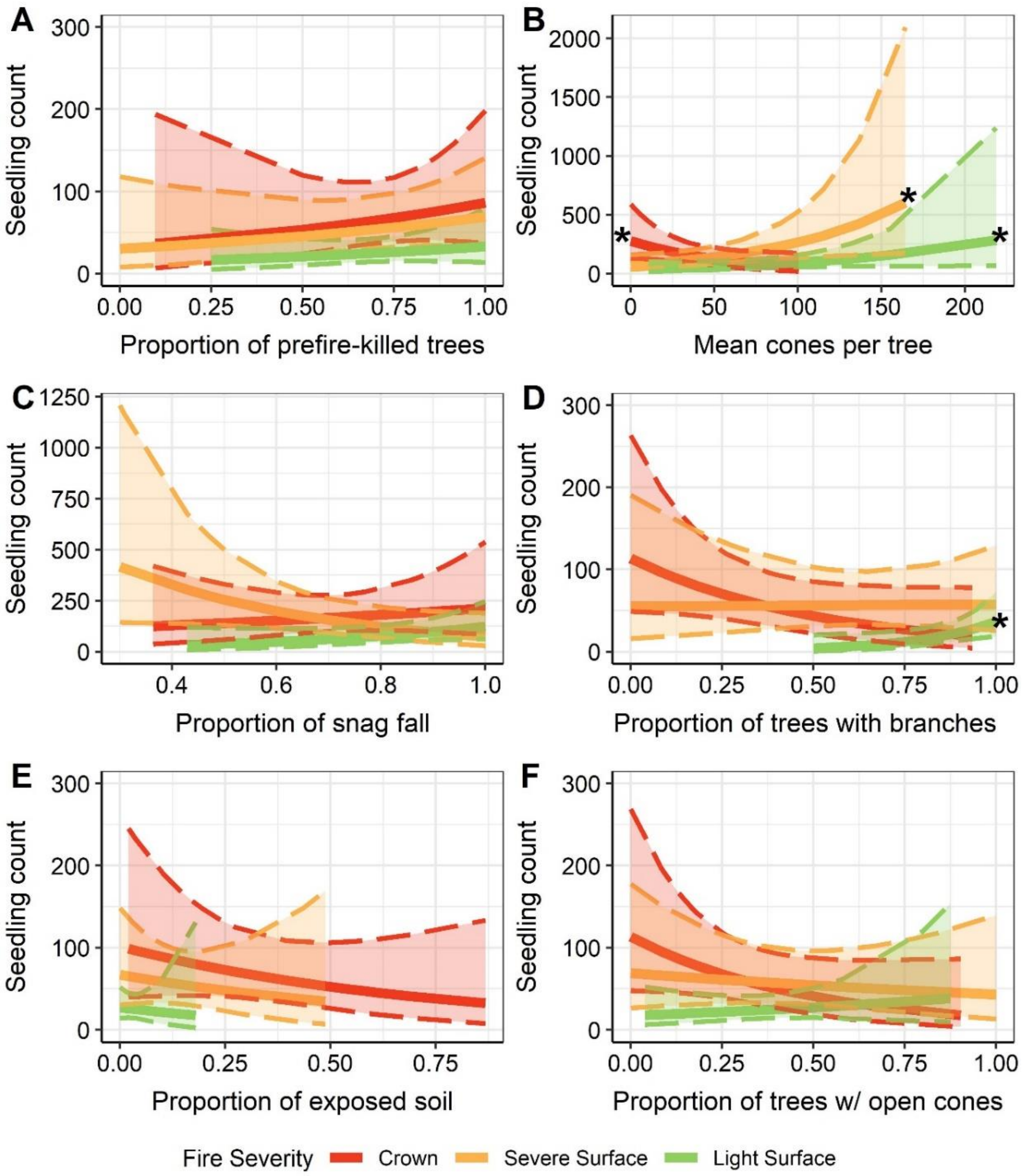

Figure 3.3. Drivers of seedling recruitment across fire severity with statistical significance noted by an *. The proportion of prefire killed trees exhibited no evidence of an effect on recruitment (**A**). Recruits declined with increasing mean cones per tree/snag in plots that experience crown fire and increased with increasing cones per tree in plots that experienced light surface fire (**B**). Snag fall exhibited no evidence of a relationship with recruitment, and plots that experienced severe surface fire, showed a declining relationship with increasing snag fall, although not statistically significant, the effect size is large (**C**). Only plots that experience light surface fire, showed evidence of an effect of proportion of trees with remaining branch structure on seedling recruitment (**D**). The proportion of exposed soil (**E**) and trees with open cones (**F**) show no evidence of an effect on recruitment. Model estimates are in Table 3.S4.

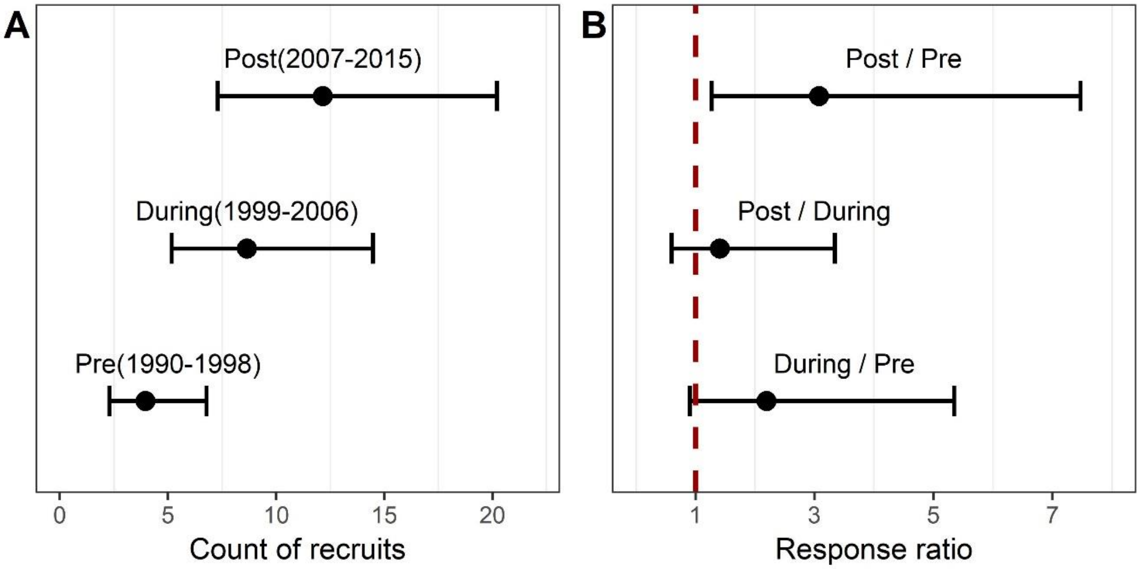

Figure 3.4. An examination of recruits during establishment periods: pre-outbreak (1990-1998), during outbreak (1999-2006), and post outbreak (2007-2015) in fire refugia. Estimated mean count of seedlings per plot that established pre, during, and post outbreak are shown in **A** with estimated 95% confidence intervals. The difference between establishment periods is shown in **B** with 95% confidence intervals with a red dashed line at one, which indicates no difference between the groups. Model estimates and response ratios are in Table 3.S5.

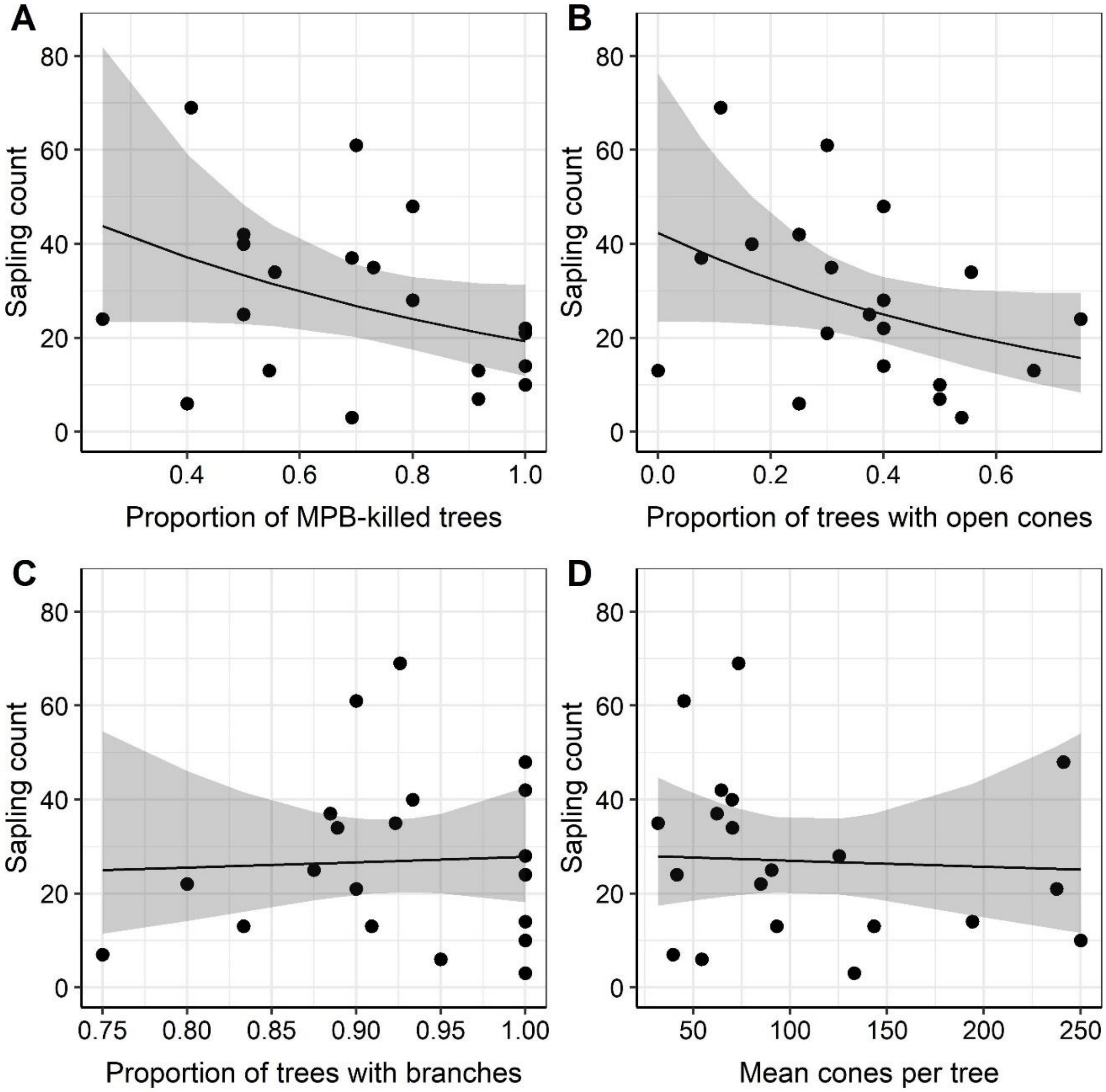

Figure 3.5. Recruitment in unburned plots as a function of stand breakdown including outbreak severity, remaining branches, open cones, and mean cones per tree/snag in fire refugia. There was no evidence of a statistically significant effect on recruitment from any of the stand breakdown variables. Recruitment declined with increasing outbreak severity (**A**). Recruitment declined with increasing cone opening (**B**). Recruitment was unrelated to the proportion of trees with branches (**C**). Recruitment was unrelated to the average number of cones per stem (**D**). Model estimates are in Table 3.S6.

Appendix

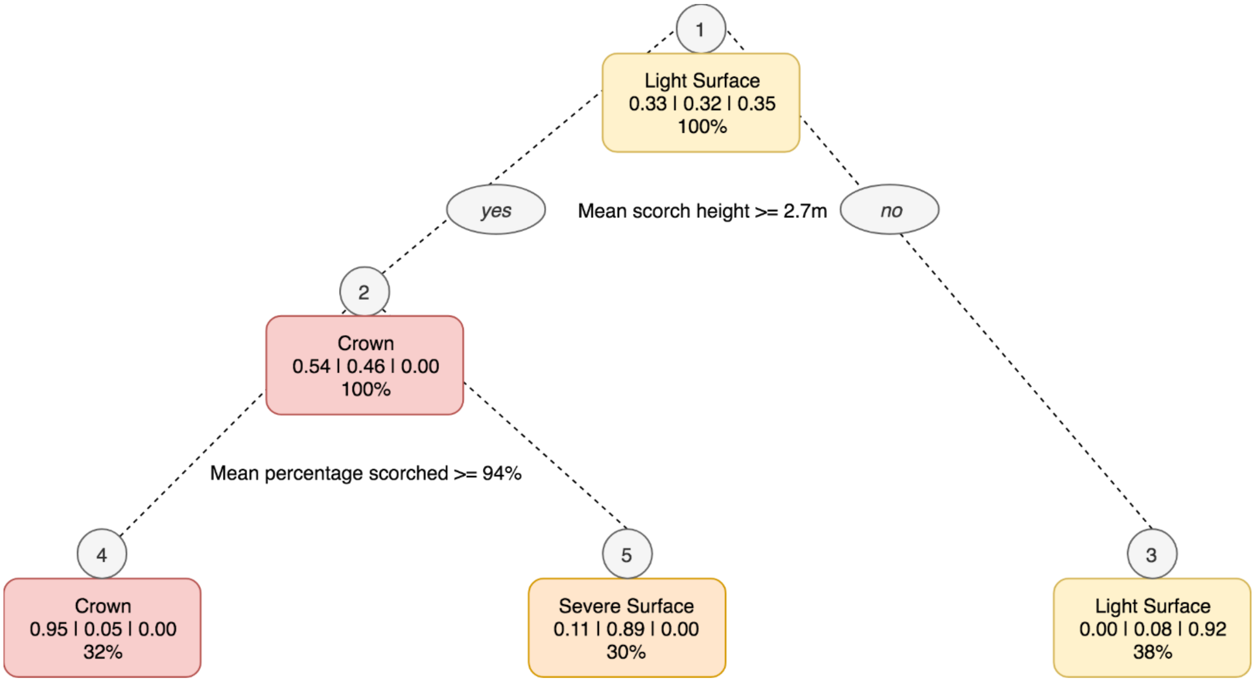

Figure 3.S1. Classification of fire severity. We used a classification tree and scatter plots to assess our visual field classification of fire severity with described fire effects measured in the field. The classification tree shows variables of importance, scorch/char height and percent of area covered by scorch/char. Within each box, we have the fire severity class – crown, severe surface, and light surface. The proportion of plots in each class are quantified in each box and from left to right refer to crown, severe surface, and light surface fire severity classes. The proportions show some fuzziness between adjacent classes in the classification.

Table 3.S1. Criteria to identify a tree's cause of death to characterize MPB outbreaks and fire mortality. Adapted from Harvey et al. (2014a). We sampled 943 canopy trees in burned plots (n=63) and 248 canopy trees in unburned plots (n=20) that totaled 1191 canopy trees.

Cause of Death Classification	Description	Trees Sampled (%)
Live tree	Live when sampled; green canopy; no visible insect activity	3.7
Fire-killed	Dead when sampled; scorched bark, branches, and/or outer sapwood; no evidence of galleries or exit holes from MPB or other bark beetle activity; not highly decayed/weathered particularly at the base and in the canopy	22.9
MPB-killed	Dead when sampled; no needles remaining in the canopy; vacated MPB galleries in cambium with exit holes in remaining bark; and in burned plots included varying degrees of scorch and deep char	60.4
Other-killed	Dead when sampled; highly decayed/weathered, no bark, missing branches; more advanced decay then MPB killed trees; or full deep char with no identifiable vacated MPB galleries	6.9

Table 3.S2. Estimated changes to stand structure and the number of recruits across all three fires that burned through gray-phase outbreak conditions. Estimates are included for pre-outbreak, post-MPB outbreaks, all prefire mortality, fire mortality, and cumulative disturbance of MPB, across both burned (burn plots *n*=63 and unburned plots *n*=20). We included estimated basal area, stem density, quadratic mean diameter (QMD), and percent of lodgepole pine. We estimated pre-outbreak conditions based on all trees/snags that were standing prior to wildfire and beetle outbreak.

	Variable measured	Mean	SD	Range
Pre-outbreak	Live basal area (m^2/ha)	24.1	11.0	5.1-58.5
	Live stem density (stems/ha)	1435	785	200-4200
	QMD (cm)	15.4	3.9	9.9-34
	Lodgepole pine (%)	96.9	8.0	63.6-100
MPB mortality	Basal area (m^2/ha)	17.7	11.4	0-55.3
	Stem density (stems/ha)	866	554	0-2200
	QMD (cm)	15.0	6.2	0-34.0
	Lodgepole pine (%)	64.4	30.6	0-100
All prefire mortality	Basal area (m^2/ha)	18.6	10.7	0-55.3
	Stem density (stems/ha)	965	532	0-2400
	QMD (cm)	15.7	4.7	0-34.0
	Lodgepole pine (%)	71.1	24.7	0-100
Fire mortality	Basal area (m^2/ha)	3.7	4.6	0-23.3
	Stem density (stems/ha)	328.9	491.3	0-2800
	QMD (cm)	7.8	6.7	0-18.3
	Lodgepole pine (%)	17.6	22.7	0-100
Cumulative mortality	Basal area (m^2/ha)	22.4	10.8	4.5-55.3
	Stem density (stems/ha)	1294	712	100-3900
	QMD (cm)	15.6	4.1	9.9-34.0
	Lodgepole pine (%)	88.3	16.5	25-100
Recruits	Total recruit density	12,202	23,400	0-170,000
	Recruit density – Crown fire	17,224	224,545	192-103,457
	Recruit density – Severe surface fire	18,804	37,760	385-170,000
	Recruit density – Light surface fire	8,715	11,407	0-37,500
	Recruit density – Fire refugia	2,765	1,869	300-6,900

Table 3.S3. Analysis of mean recruitment across fire severity classes and comparisons between fire severity classes per plot. The response ratios are calculated from the estimates. Estimates and response ratios are reported with 95% lower and upper confidence intervals, LCI and UCI respectively. Table corresponds to Figure 3.2.

	Estimate	LCI	UCI	Comparison	Response Ratio	LCI	UCI	p-value
Crown	97.63	60.76	156.87	Crown / Severe Surface	0.91	0.37	2.26	0.99
Severe Surface	107.27	66.24	173.71	Crown / Light Surface	2.13	0.89	5.07	0.10
Light Surface	47.92	29.61	71.21	Crown / Fire Refugia	6.24	2.41	16.17	**<0.0001**
Fire Refugia	15.65	9.27	26.45	Severe Surface / Light Surface	2.34	0.97	5.62	**0.05**
				Severe Surface / Fire Refugia	6.86	2.63	17.89	**<0.0001**
				Light Surface / Fire Refugia	2.94	1.17	7.37	**0.011**

Table 3.S4. Regression analysis testing the relationships between seedling recruitment and our contributing factors in burned plots. Contributing factors included canopy architecture, outbreak severity, soil, snag fall, and postfire climate. Estimates and confidence intervals (CI) have been exponentiated back to the scale of the data and estimates correspond to on unit change. Table corresponds to Figure 3.3 and Figure 3.S2.

Contributing Factor	Fire Severity	Estimate	95% CI		p-value	Figure
			Lower	Upper		
Prefire mortality	Crown	2.59	0.07	80.66	0.446	3.3-A
Prefire mortality	Severe surface	0.88	0.017	45.85	0.936	3.3-A
Prefire mortality	Light surface	0.97	0.013	83.22	0.988	3.3-A
Cone abundance	Crown	0.98	0.97	1.003	**0.043**	3.3-B
Cone abundance	Severe surface	1.029	1.008	1.050	**0.003**	3.3-B
Cone abundance	Light surface	1.026	1.002	1.05	**0.008**	3.3-B
Snag fall	Crown	2.30	0.103	48.81	0.572	3.3-C
Snag fall	Severe surface	0.037	0.0009	1.56	0.086	3.3-C
Snag fall	Light surface	4.31	0.059	253.15	0.482	3.3-C
Branch structure	Crown	0.146	0.015	1.92	0.066	3.3-D
Branch structure	Severe surface	7.14	0.28	135.9	0.146	3.3-D
Branch structure	Light surface	573.7	3.91	57661.9	**0.004**	3.3-D
Soil exposure	Crown	0.27	0.009	7.48	0.269	3.3-E
Soil exposure	Severe surface	0.97	0.006	356.9	0.989	3.3-E
Soil exposure	Light surface	0.36	0.000001	1180929	0.847	3.3-E
Open cones	Crown	0.13	0.008	2.91	0.084	3.3-F
Open cones	Severe surface	4.82	0.12	173.2	0.292	3.3-F
Open cones	Light surface	19.08	0.49	671.2	0.095	3.3-F
Frost events	Crown	0.99	0.94	1.04	0.528	3.S2
Frost events	Severe surface	0.99	0.94	1.04	0.557	3.S2
Frost events	Light surface	0.98	0.94	1.03	0.437	3.S2
Snow accumulation	Crown	0.93	0.88	0.98	**0.012**	3.S2
Snow accumulation	Severe surface	0.93	0.88	0.98	**0.012**	3.S2
Snow accumulation	Light surface	0.93	0.88	0.98	**0.008**	3.S2
Climate moisture deficit	Crown	0.99	0.97	1.004	0.155	3.S2
Climate moisture deficit	Severe surface	0.99	0.97	1.003	0.13	3.S2
Climate moisture deficit	Light surface	0.98	0.97	1.002	0.097	3.S2

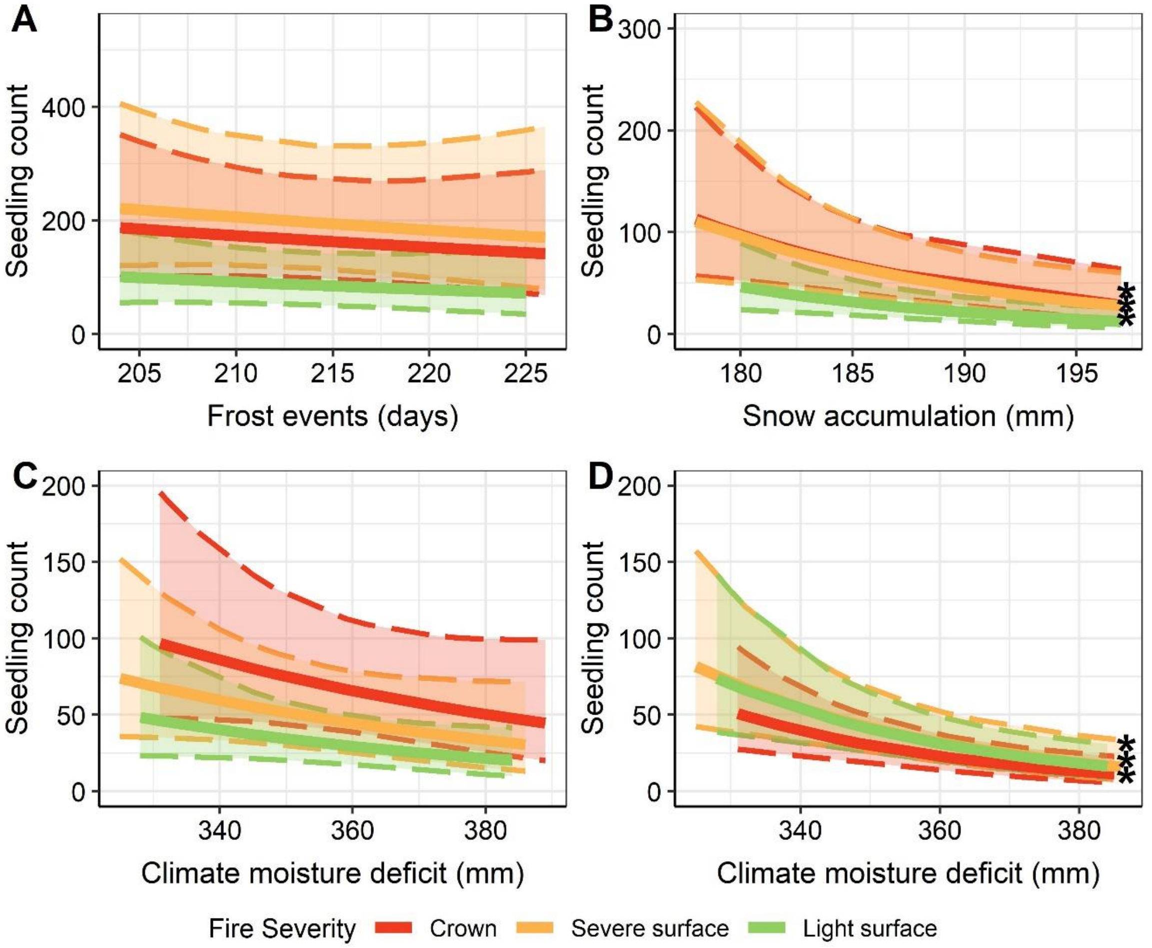

Figure 3.S2. The effect of postfire climate on seedling recruitment. Statistical analyses indicated no measureable evidence of an effect for total frost days (**A**), snow accumulation (**B**), or climate moisture deficit (CMD; **C**). There were three prominent outliers of seedling counts that we removed and reran the analyses. CMD was the only relationship that changed to show statistical evidence of a relationship with a decline in recuitment corresponding to increasing climate moisture deficit (**D**) with * indicating statistical significance. Figure corresponds to Appx. Table 3.S4.

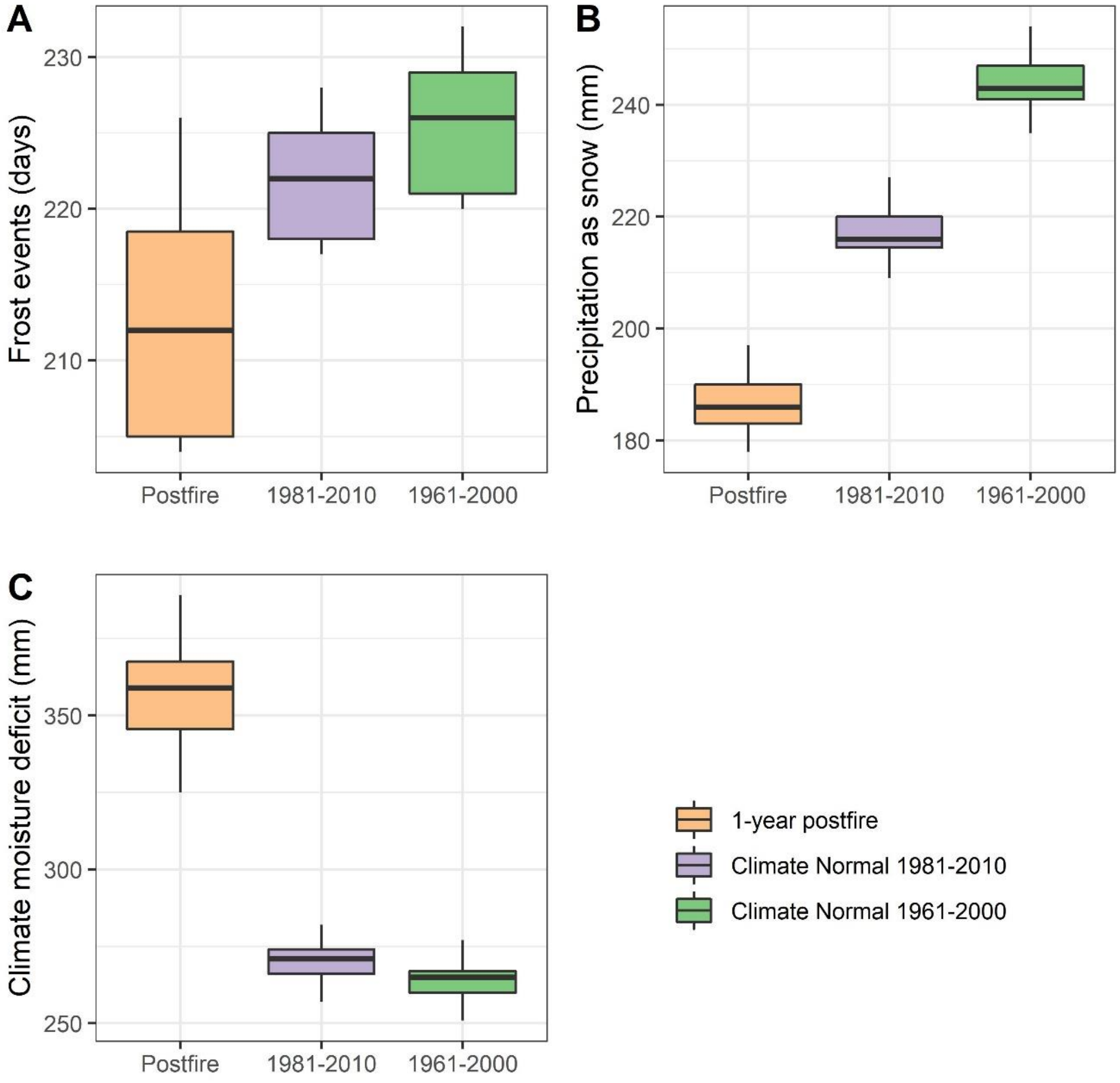

Figure 3.S3. Boxplots showing the difference between one-year postfire climate variables compared to climate normal variables for both 1961-2000 and 1981-2010. One-year postfire climate variables are different from climate normal variables for both 1961-2000 and 1981-2010, generally suggesting warmer and/or drier conditions.

Table 3.S5. Analysis of mean recruitment for establishment periods during the MPB outbreak: pre-outbreaks, during outbreaks, and post outbreaks and comparisons between the establishment periods per plot. The response ratios are calculated from the estimates. Estimates and response ratios are reported with 95% lower and upper confidence intervals, LCI and UCI respectively. Table corresponds to Figure 3.4.

Explanatory Variable	Estimate	95% CI		Comparison	Ratio	95% CI		p-value
		Lower	Upper			Lower	Upper	
Pre (1990-1998)	3.95	2.30	6.78	During/Pre	2.19	0.88	5.45	0.099
During (1999-2006)	8.65	5.17	14.48	Post/ Pre	3.08	1.24	7.61	**0.008**
Post (2007-2015)	12.15	7.31	20.21	Post /During	1.40	0.58	3.40	0.63

Table 3.S6. Regression analysis testing the effect of contributing factors: canopy architecture and MPB outbreak severity on seedling recruitment in unburned plots. Analyses was conducted with generalized linear models using a negative binomial distribution. This table corresponds to Figure 3.5.

Explanatory Variable	Estimate	95% CI		p-value	Figure
		Lower	Upper		
Proportion of MPB-killed trees	0.34	0.083	1.33	0.0899	3.5-A
Proportion of trees with open cones	0.27	0.058	1.31	0.0763	3.5-B
Proportion of MPB-killed trees	0.42	0.11	1.47	0.1619	3.5-B
Proportion of trees with branches	1.53	0.014	163.40	0.8412	3.5-C
Proportion of MPB-killed trees	0.34	0.082	1.42	0.1103	3.5-C
Average cones per tree	0.9995	0.995	1.004	0.848	3.5-D
Proportion of MPB-killed trees	0.36	0.071	1.92	0.194	3.5-D

CHAPTER 4: Landscape-scale assessment of burn severity for sub-boreal forests with bark beetle outbreaks in British Columbia

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Keywords: Wildfire, Mountain Pine Beetle, British Columbia, Google Earth Engine, Boosted Regression Trees, disturbance interactions, remote sensing, NDVI, NDMI, RdNBR

Abstract

Bark beetle outbreaks and wildfire are two of the most prevalent disturbances in North American forests that influence tree mortality, regeneration, and successional trajectories. Contemporary forests are experiencing overlaps in these disturbances, where wildfire is burning through landscapes with substantial tree mortality from outbreaks. It is unclear if substantial tree mortality from outbreaks influences burn severity in sub-boreal forests. We generated spatial data from Landsat imagery for three fires in 2012, 2013, and 2014 in central interior British Columbia, Canada. We characterized outbreak severity conditions, prefire vegetation conditions, and subsequent burn severity that were measured with spectral indices. We then evaluated drivers of moderate-high burn severity under moderate and high fire weather conditions with boosted regression tree statistical modeling. Landsat-based spectral indices of outbreak severity and prefire vegetation conditions indicated gradients of forest structure and composition associated with dead/sparse, to a mixture of live and dead, to live/dense forest vegetation. Burned areas were dominated by high burn severity, indicating that most of the landscape still burns at high severity even with substantial prefire mortality. Prefire vegetation conditions and fire weather ranked as the top two variables of influence in both models and indicated that high probability of high burn severity was associated with a mixture of live and dead forest vegetation. Fire weather was ranked highest in the high fire weather model and second in the moderate fire weather model supporting the notion that fire weather is a key driver in these large infrequent fire systems and corresponds with drier conditions associated with these fire years. This study illustrates how prefire vegetation conditions and fire weather creates an environment that is conducive for wildfire across sub-boreal forest with pervasive tree mortality from beetle outbreaks.

Introduction

Understanding the role of fuels, weather, and topography on burn severity is crucial for anticipating how these variables may interact under future climate scenarios, forest conditions, and disturbance regimes. Across western North America, many fire-prone subalpine, sub-boreal, and boreal forests are shaped by wildfire events that result in substantial high burn severity driven by a favorable fire environment where climatic conditions reduce fuel moisture (Krawchuk and Moritz 2011). On contemporary landscapes, sub-boreal and subalpine forests have substantial tree mortality from recent mountain pine beetle outbreaks (MPB; *Dendroctonus ponderosae*) (Raffa et al. 2008, Axelson et al. 2009, Perrakis et al. 2014), altering the composition and structure of prefire vegetation (i.e., configuration of fuels) that may influence burn severity. Burn severity, from a satellite-based remote sensing perspective, is ultimately capturing changes in spectral reflectance that can be linked with immediate fire effects such as tree mortality and changes in canopy structure (Keeley 2009). Landscape-scale assessments that have evaluated the relationship between insect outbreaks and wildfire indicate that changes in vegetation composition and structure do not elicit a strong control on fire activity (Hart et al. 2015, Meigs et al. 2015, 2016). Field-based assessments have either found little to no effect of outbreak severity on measures of immediate fire effects (Talucci and Krawchuk 2019, Harvey et al. 2014a, 2014b, Agne et al. 2016) or that outbreak severity increases the consumption of woody biomass that alters legacy structures across the postfire landscapes (Talucci and Krawchuk 2019). Satellite-based research has not evaluated the relationship between outbreak severity and wildfire at the core of the MPB outbreak, where lodgepole pine dominates and MPB-induced mortality is the most extensive in western North America. Understanding what drives burn severity in sub-boreal forests with substantial MPB-induced mortality under gray-phase conditions across British Columbia, Canada can complement existing field-based research and support adaptive forest management.

Burn severity is driven by climate and weather conditions, topography, and prefire vegetation structure and composition. Climate conditions that generate high pressure blocking systems create hot, dry conditions or recurrent drought conditions that prime landscapes for wildfire events, particularly in subalpine, sub-boreal, and boreal ecosystems (Nash and Johnson 1996, Schoennagel et al. 2004), which all share life zones and exhibit similarities in forest composition and structure (Holdridge 1947). In subalpine forests, fuels become relatively less important as a controlling variable when fire weather becomes extreme (Bessie and Johnson 1995), while under moderate fire weather conditions, fuels may be more important for burn severity. The blocking high pressure systems over the continent generally correspond to teleconnection patterns such as the Pacific Decadal Oscillation, El Nino Southern Oscillation, and Artic Oscillation (Macias Fauria and Johnson 2008). For infrequent high-severity fire regimes in the northern US Rocky mountains, trends for contemporary fire activity (1984-2010) show that the proportion of high-severity patches increased as the size of the fire increased, which is driven by climate and weather conditions (Harvey et al. 2016). In the US Pacific Northwest, high-severity patch size was shown to increase with fire extent and associated drought conditions over time (Reilly et al. 2017). Other research has shown that topography and weather can both be important drivers of high burn severity in mountainous landscapes (Dillon et al. 2011).

Recent, large-scale insect outbreaks have affected western North American conifer forests, altering vegetation and fuel conditions on fire-prone landscapes, which has created concern for how these landscapes will burn. Changes in fuel structures are associated with potential fire behavior (Hicke et al. 2012) and subsequent burn severity (i.e., fire-induced ecosystem change). Recent landscape-scale assessments have evaluated the influence of outbreak severity on fire activity across subalpine forest in the western United States (US; Hart et al. 2015, Meigs et al. 2015, 2016). During extreme fire years, area burned was found to be unaffected by the extent of MPB outbreaks in forests across the western US (Hart et al. 2015). Fire likelihood was found to be unaffected by previous tree mortality from MPB outbreaks across dry conifer forests in the US Pacific Northwest without accounting for fire weather (Meigs et al. 2015). Burn severity was found to be diminished by outbreak severity in the US Pacific Northwest at the scale of the fire event (Meigs et al. 2016). These studies have been limited in how they account for fire weather, which makes it challenging to infer the potential effect of outbreak mortality on burn severity and evaluate the full fire environment.

The composition and structure of prefire forest vegetation can consist of gradients of mostly alive to mostly dead trees as well as sparse to dense canopy structure, particularly on landscapes with substantial prefire insect mortality. Evaluation of burn severity metrics on landscapes with prefire tree mortality suggest some uncertainty regarding the relationship between burn severity and prefire mortality conditions from insect outbreaks, specifically discrepancies between field observations and satellite-measured change (McCarley et al. 2017, Harvey et al. 2019). Contemporary sub-boreal forest conditions are characterized by wildfire burning through forested landscapes with substantial volume of standing snags (i.e. dead standing trees) and fallen deadwood from these recent outbreaks, which can burn differently than live trees (Talucci and Krawchuk 2019), influencing subsequent fire effects. Previous landscape-scale assessments have focused on the western US (Hart et al. 2015, Meigs et al. 2015, 2016) and evaluated MPB-fire interactions at the scale of the fire event (Meigs et al. 2016) with limited evaluation at the scale of a Landsat pixel, 30m × 30m, or without accounting for variability in fire weather (Hart et al. 2015, Meigs et al. 2015). It is challenging to infer ecological effects at the scale of the fire event due to the inherent heterogeneity that exists across landscapes and within fire events (Parks et al. 2018). Burn severity and postfire burn mosaics are dependent on the existing landscape patterns and subsequent interaction within the fire environment – fuels, weather, and topography (i.e. fire behavior triangle), which vary throughout the life of a fire. The gradients of outbreak severity, fire weather conditions, and burn severity within the fire mosaic have not received the full attention in previous studies (Hart et al. 2015, Meigs et al. 2015, 2016).

In British Columbia, sub-boreal forests are dominated by lodgepole pine that historically burned with a substantial portion of high-severity and has experienced pervasive mortality from recent MPB outbreaks. Recent fires have burned through large portions of these forests with pervasive tree mortality, providing an opportunity for a 30m × 30m pixel wise assessment to evaluate local variability of burn severity within fire events that were largely unmanaged and included a variety of weather conditions. Here we assess the relative influence of a suite of drivers on the variability in burn severity. Our work involved two objectives: (1) develop spatially explicit estimates of outbreak severity, prefire vegetation conditions, fire weather, and topography at 30m-by30m pixel scale; (2) evaluate the drivers of high burn severity across outbreak-affected forests while accounting for fire weather conditions, prefire vegetation associated with MPB, and topography. We characterized outbreak severity during the red phase as an indicator of outbreak extent and severity, which would have been ecologically distinct as snags with red needles retained in the canopy in contrast to the post-outbreak early successional forest structure associated with prefire vegetation conditions in the gray phase (Hopkins 1909, Hicke et al. 2012). We expected that these ecologically discrete periods would be spectrally distinct and could inform our evaluation of fuel conditions as potential drivers of burn severity. However, we anticipated that fuels would have a relatively low influence on burn severity compared to fire weather, such as hot, dry, and windy conditions conducive to large infrequent fire events on these landscapes. We also anticipated that high fire weather would have greater influence on high burn severity in comparison to moderate fire weather conditions.

Methods

Study Area

Our study area included the footprints of three wildfires that burned in 2012, 2013, and 2014 within the boundaries of two provincial parks – Tweedsmuir and Entiako – located in the central interior of British Columbia (Figure 4.1). Based on climate normals from 1981-2010, total annual precipitation for the region is 507.6 mm with snowfall during winter months and a mean monthly maximum temperature of 8.5°C (range: -3.3-19.8°C; Abatzoglou et al. 2018). Annual climate moisture deficits for the fire years indicate conditions that are drier than climate normals for 1981-2010 (Figure 4.A1; Wang et al. 2012). Landscapes are gently rolling and associated with the sub-boreal spruce and sub-boreal pine-spruce biogeoclimatic zones (Meidinger and Pojar 1991). Moisture gradients and disturbance history dictate forest composition and structure (Delong 1998), with patches of pure lodgepole pine inhabiting the driest portions of the moisture gradient and enduring with fire return intervals of 100-150 years (Parminter 1992), patches of seral lodgepole pine communities with understories and mixed canopies of subalpine fir (*Abies lasiocarpa*) and spruce hybrid (*Picea engelmannii* x *glauca*) that persist with longer fire return intervals, and patches of pure spruce in areas of high moisture and long periods without fire (Cichowski and Morgan 2009). Prior to the recent fires, these forests had experienced substantial tree mortality from recent MPB outbreaks (1990s and 2000s), generating gradients of live and dead forest composition and structure. Fires occurred when outbreak mortality was in the gray phase, over a decade after the peak of the outbreak, where snags had dropped their needles, started to slough their bark, and partially transitioned to downed coarse wood through tree fall (Hicke et al. 2012). These prefire forests contained a mixture of live and dead trees in the canopy, the sub-canopy having low density spruce, subalpine fir, and lodgepole, and forest floor covered by mosses, lichens and low growing shrubs e.g., kinnikinnik (*Arctostaphylos uva-ursi*; *-pers.obs.* Anna Talucci). Due to the location of these fires in provincial parks, they all burned under ‘modified response’ (i.e. for resource benefit), with suppression only focused on a few hunting cabins within the area and at the borders where provincial parks abutted lands managed for timber production. They varied in size: the Entiako fire (R10171) burned 7,000 ha in 2012; the Tweedsmuir fire (R10252) burned 3,000 ha in 2013; and the Chelaslie fire (R10070) burned 130,000 ha in 2014.

Spatial data

The fires burned under a variety of fire weather conditions and over a range of MPB outbreak severity. We generated spatial data for MPB outbreak severity, prefire vegetation conditions, burn severity, and topographic variables (Figure 4.A2) using Google Earth Engine (GEE). Outbreak severity conditions were characterized during the red phase, which was based on observation (Goodwin et al. 2008, Wulder et al. 2009) and available data (BCMFLNRO 2016) for the area. Prefire vegetation conditions were from one year prior to fire. Burn severity was estimated from the difference between one-year prefire and one-year postfire for each fire following the extended assessment outlined by Key and Benson (2006). To characterize red-phase outbreak severity conditions, prefire vegetation conditions, and burn severity, we used vegetation indices based on surface reflectance imagery from Landsat 5, 7, and 8, from 1984 through 2015 and focused on growing season months, June through September. The Landsat series – i.e. Landsat 5-Thematic Mapper (TM), 7-Enhanced Thematic Mapper (ETM+), 8-Operational Land Imager (OLI) – was harmonized following the calibration data from Roy et al. (2016) to create corresponding sensor bands between Landsat 8-OLI and Landsat 7-ETM+. This calibration allowed us to work seamlessly across the Landsat series for all analyses. A cloud mask was applied to minimize the effect of pixels covered by clouds and was generated from the "CFMASK" attribute, which is included as part of the Landsat Surface Reflectance Tier 1 products. For each Landsat image, we calculated four spectral vegetation indices: Normalized Burn Ratio (NBR), Normalized Difference Vegetation Index (NDVI), Normalized Difference Moisture Index (NDMI), and Enhanced Vegetation Index (EVI) based on equations described in Table 4.1. These indices measure conditions associated with vegetation conditions, photosynthetic activity, phenology, and moisture content that can differentiate between live and senesced/dead vegetation (e.g. Goodwin et al. 2008, Meigs et al. 2011, Kennedy et al. 2012, Brodrick et al. 2017). Across our study region, data gaps were a significant issue either due to Landsat 7 scan line errors and/or cloud coverage. We mitigated this issue by generating composite images where needed with the best pixel approach (Hermosilla et al. 2015). For topographic variables, we used the Canadian Digital Elevation Model from Natural Resources Canada altimetry system acquired through GEE. We extracted aspect, slope, and elevation to calculate an index called 'aspect transformation in site productivity research' (ATSPR; Beers et al. 1966) and topographic position index (TPI) of 450m. We anticipated that topography would not exert a strong influence on the probability of high burn severity due to the gently rolling landscape.

To characterize outbreak severity during the red phase, we calculated the difference in NDMI per pixel between pre-outbreak (1995) and post-outbreak (2006), represented as the difference NDMI (dNDMI). The pre-outbreak year, 1995, was based on the imagery that was available prior to outbreak where NDMI values were stable and had not started to decline. Between 2000 to 2006 area impacted by MPB attack increased (Wulder et al. 2009) and by 2006 many of these areas exhibited red-phase conditions, where the needles of MPB attacked trees turn red (Goodwin et al. 2008). Previous research has assessed the accuracy of the NDMI metric to determine the year a stand dies from MPB attack in the Morice Timber Supply Area to the northwest of our study area (Goodwin et al. 2008), which likely exhibited similar outbreak conditions. The NDMI metric has been used to characterize tree mortality associated with MPB outbreaks in the US (Walter and Platt 2013, Cartwright 2018). We opted to characterize outbreak severity in the red phase, when tree mortality has occurred and canopies have turn red after MPB attack (Hicke et al. 2012). Because tree canopies in the red phase obscure the green vegetation in the under-story, our estimates likely capture the greatest extent of forests affected by the outbreaks. As an ancillary investigation of the outbreak’s progression, we used a spectral time series of the NDMI values from 1984 to 2017 and applied the LandTrendr segmentation algorithm (described below) to estimate the decline in spectral values associated with MPB-attack and red-phase outbreak conditions (Figure 4.3). Due to the spatiotemporal progression of outbreaks, tree mortality varies over time, which is why we calculated the difference between pre-outbreak NDMI values and red-phase outbreak NDMI values to represent outbreak severity.

Prefire conditions in mature sub-boreal forests were characterized by substantial tree mortality from MPB and other agents, a combination of snags with some surviving canopy trees, some places with sub-canopy subalpine fir and spruce, and forest floor covered with low growing mosses, lichens, forbs, and shrubs that are supported by the moist, cool environment. We used prefire NDVI as the explanatory variable for prefire vegetation conditions in the statistical models based on an exploratory analysis, described below. Prior research evaluating drivers of burn severity has characterized prefire vegetation with a number of indices that can describe vegetation conditions including NDMI, EVI, NDVI, and NBR (e.g. Kennedy et al. 2012, Meigs et al. 2016, Brodrick et al. 2017, Parks et al. 2018). All indices take advantage of the near-infrared band, which tends to be sensitive to the cell structure of leaves and is used as an indicator of photosynthetic activity in plants. We evaluated the Pearson's correlation between the variables generated from Landsat (NDVI, dNDMI), and found that NDVI was only moderately correlated with dNDMI (-0.43).

We used high-resolution aerial imagery collected in 2012 (GeoBC 2012) to independently assess and interpret the NDVI values as they related to vegetation conditions on the ground. We visually inspected 150 randomly selected sites from the full random sample (n=60,800; described below) for evidence of tree mortality and tree density. Visual inspection of the aerial imagery with associated NDVI values showed a range of variability and a general decline in values with increasing tree mortality associated with the MPB outbreaks and/or sparser vegetation (Figure 4.A5).

We calculated burn severity based on prefire and postfire NBR images as the Relative differenced Normalized Burn Ratio (RdNBR; see Miller and Thode 2007) and classified the continuous RdNBR data into bins based on field observations within the study fires. NBR-based metrics of burn severity, RdNBR and dNBR (differenced Normalized Burn Ratio; Key and Benson 2006), have been compared with mixed findings, e.g., that RdNBR demonstrates a better relationship with field data (Whitman et al. 2018, Harvey et al. 2019), while dNBR corresponds better to structural changes measured by light detecting and ranging (LIDAR) metrics (McCarley et al. 2017). Both indices do a better job of capturing canopy-associated change from fire than change associated with the forest floor beneath the canopy since satellites provide a top-down perspective of forested landscapes (Kolden et al. 2012). Evaluations have expressed some uncertainty in the accuracy and overestimation of burn severity on landscapes where wildfire is preceded by MPB outbreaks that reduce canopy cover prior to fire (McCarley et al. 2017, Harvey et al. 2019). We used field measurements of fire effects collected two to four years postfire in 2016 from plots across all three fires (Talucci et al. 2019 [This dissertation, Chapter 3]) and composite burn index (CBI) field metrics from the Entiako fire collected one-year postfire in 2013 (data collected by Krawchuk) to inform break points in burn severity classes. Evaluation of field-based fire effects and classifications indicated that RdNBR values ≥ 600 overlapped with moderate to high burn severity classes that were based on field data collected two to four years postfire and corresponded to a clear break in the CBI data (Figure 4.A3). As such, we classified the RdNBR images as presence/absence (1/0) of high burn severity with high burn severity categorized as RdNBR ≥ 600.

Fire Weather

We used day of burn maps to extract fire weather variables and assign burning conditions to each pixel of each fire, using MODIS hot spot data to generate day-of-burn progression maps (Parks 2014). We linked day-of-burn maps to the daily Fire Weather Index (FWI) that is calculated from seasonal and daily temperature, relative humidity, and wind speed acquired from the nearest weather station. Weather stations used to calculate the FWI were located at distances 30-70 km from burned pixels. FWI is part of the Canadian Forest Fire Weather Index System (Van Wagner 1987) and a standard metric for characterizing fire weather. We split FWI into two categories – moderate (>13–29) or high (>29) – based on breakpoints outlined by Alexander and De Groot (1988). We had few days that registered as benign burning conditions (0-13; Figure 4.2).

Sampling

We randomly sampled individual 30m × 30m pixel locations across forested areas within our three fire perimeters. Sample points were generated for five percent of each fire extent after Parks et al. (2018), providing a large sample size for analysis (total sample n=60,800). We only sampled forested areas because we were interested in burn severity in forested landscapes affect by MPB outbreak. Forested areas were identified with the Vegetation Resource Inventory (VRI; BCMFLNRO 2012), a government data product produced from aerial imagery and field data. The random sample of locations was selected using a generalized random-tessellation stratified (GRTS) design with the “spsurvey” package (Kincaid and Olsen 2017) in R Statistical Computing Software (R Development Team 2018). GRTS generates spatially random sampling design (Stevens and Olsen 2004). We used the sampled points from the GRTS to extract values from all spatial layers in the image stack in GEE listed in Table 4.1.

Analyses

We characterized temporal trends in spectral indices associated with the MPB outbreaks and determined the drivers and characteristics of high burn severity. We used LandTrendr (LT) applications in GEE (Kennedy et al. 2018) to apply a time series segmentation algorithm (Kennedy et al. 2010) to NDMI values that characterized outbreak severity conditions. We sampled pixels from the full available times series, 1984-2017. Samples were selected based on VRI forested areas with a majority of lodgepole pine from within each fire perimeter (Entiako n=53 pixel locations; Tweedsmuir n=164 pixel locations; Chelaslie n=1726 pixel locations). For each fire event, the NDMI values for each pixel were extracted from the time series of images, and a mean NDMI value was calculated for each year. The extracted annual mean NDMI values are the source values. The LT segmentation algorithm was applied to the source values to interpolate a fitted trend line for segments of stability or change for the spectral trajectory (Kennedy et al. 2018).

We evaluated the drivers of high burn severity under two fire weather conditions using boosted regression trees (BRT). Specifically, we analyzed the probability of high burn severity (presence/absence) as a function of outbreak severity, prefire vegetation conditions, fire weather, and topography under moderate (FWI >13–29) and high (FWI >29) fire weather. We split the data and models by fire weather because we wanted to be able to differentiate if the drivers of burn severity varied under different fire weather conditions. For the two models, the explanatory variables, outbreak severity (dNDMI), prefire vegetation conditions (NDVI), fire weather (FWI), and topography (elevation), were selected based on relative influence in a full model that included all possible explanatory variables described in Table 4.1 (Figure 4.5). We estimated percent of area burned by burn severity classes, moderate-high (RdNBR ≥ 600) and low-unchanged (RdNBR < 600), using landscape metrics from the ‘SDMTools’ package (VanDerWal et al. 2014) in R Statistical Computing Software (R Development Team 2018).

All analyses were performed in the R Statistical Computing Software (R Development Team 2018). We fit the BRT model with ‘gbm’ (Ridgeway 2015) and ‘dismo’ (Hijmans et al. 2016) packages. The use of BRT models for analysis allowed for the integration of various data types, handling of nonlinear relationships, and discerning patterns amongst noisy ecological data (De’ath and Fabricius 2000), while also allowing for interaction effects (Elith et al. 2008). We adapted our script from Elith et al. (2008) and Krawchuk et al. (2016) and used recommended BRT options (bagging fraction=0.5, learning rate=0.05, tree complexity =3) from Elith et al. (2008). We assessed the model fit based on the area under the receiver operator characteristic (AUROC) curve. We used the relative influence of explanatory variables and the shape of the relationship to infer associations with high burn severity. The relative influence of explanatory variables was scaled to sum to 100 (Friedman 2001). Data and code for analyses are available online (Talucci 2019).

Results

MPB outbreaks: spatial data assessment

The range and variability of NDVI (the metric for prefire vegetation condition) corresponded to gradients of outbreak severity and vegetation densities in the high-resolution aerial imagery, while the range of dNDMI (the metric for outbreak severity conditions during the red-phase) parallels the range and variability of NDVI. At the high end of the NDVI values (>0.80), corresponding aerial imagery showed live, dense tree canopies (Figure 4.4, 4.5, and 4.A5), while at the lower end of NDVI values, corresponding aerial imagery indicates higher outbreak severity and/or an open canopy structure (Figure 4.4 and 4.5). Larger changes in NDMI values (>100), corresponded to moderate to high tree mortality from MPB attack in the red phase (Figure 4.5, and 4.A5). Across the landscapes, areas unaffected by MPB attack were limited (Figure 4.5). The change in NDMI values relate to the decline in mean annual NDMI values associated with the onset and progression of MPB outbreaks (Figure 4.3). Spectral trajectories decrease for over a decade, followed by an abrupt decline in mean annual NDMI values associated with wildfires followed by a rebound in the postfire years associated with vegetation regrowth and early successional forest development.

Drivers and characteristic of high burn severity

High burn severity dominated the extent of the three fires, but there was also substantial area that burned at lower severity. High burn severity was predominantly explained by variation in prefire vegetation conditions (NDVI) and fire weather (FWI). The percent of high burn severity varied within the perimeter of the study fires with 57% of the Entiako fire, 82% of the Tweedsmuir fire, and 69% of the Chelaslie fire (Figure 4.5 and 4.6). For the two BRT models representing moderate and high fire weather conditions, the high-FWI model had a slightly better fit (AUROC = 0.77; Table 4.2) compared to the moderate-FWI model (AUROC = 0.73; Table 4.2). The relative influence of explanatory variables differed between models (Table 4.2). In the moderate-FWI model, prefire vegetation conditions (NDVI) ranked first with a relative influence of 37.4% followed by fire weather (FWI) at 27.4%, elevation at 23.2 %, and outbreak severity (dNDMI) at 12.0%. In the high-FWI model, fire weather (FWI) ranked first with a relative influence of 36.4%, followed by prefire vegetation conditions (NDVI) at 27.8%, outbreak severity (dNDMI) at 21.9%, and elevation at 13.9%.

The shape of the statistical relationships for explanatory variables were consistent between models, with the moderate-FWI model generally having a reduced probability of high burn severity compared to the high-FWI model. The relationship between the probability of high burn severity and prefire vegetation conditions (NDVI) shows a ‘hump-shaped’ curve in the partial-dependence plot (Figure 4.7). High probabilities (0.7-0.85) were associated with NDVI values from 0.5 to 0.7 (Figure 4.7), with a decrease in the probability of high burn severity at higher NDVI values. The probability of high burn severity generally increased with increasing FWI (Figure 4.7). Elevation showed a variable and limited influence on the probability of high burn severity (Figure 4.7). In addition, outbreak severity (dNDMI) also exhibited a ‘hump-shape’ relationship indicating that greater change in NDMI values was associated with greater probability of high burn severity.

Discussion

Our results provide insight into the characteristics and drivers for short-interval, MPB-fire disturbances. We show that variability in prefire vegetation conditions are an important driver of high burn-severity and suggest that these prefire vegetation conditions measured by NDVI represent ecological gradients of forest structure. Prefire vegetation conditions (NDVI) and fire weather (FWI) were the top-ranked explanatory variables for discriminating between high and low burn severity in our landscapes. Locations with intermediate values of prefire vegetation conditions (NDVI) had the greatest probability of high burn severity, and the vegetation composition of these sites was a mixture of live vegetation and abundant standing deadwood from the MPB outbreaks. In contrast, locations with lower or higher NDVI values had lower probabilities of high burn severity, which suggests that areas with mostly dead or sparse vegetation and areas with dense, live canopies had lower probabilities of burning at high severity. Our results suggest that prefire vegetation conditions and fire weather are both critical drivers of burn severity for sub-boreal forests – and since those prefire vegetation conditions included gradients of pervasive tree mortality from MPB outbreak a decade earlier, the MPB legacy affects burn severity.

MPB outbreaks: spatial data assessment

The NDVI values associated with sampled data indicate gradients in prefire vegetation composition and structure that ranged from dense live canopies, to dense mixtures of live trees and snags, to sparser forest or mostly snags (Figure 4.4). Prefire vegetation conditions across the landscapes were dominated by NDVI values between 0.5-0.75, which corresponded to a combination of live trees and dead snags when visually inspected in high-resolution aerial imagery (Figure 4.4; Figure 4.A4). High probabilities of high burn severity were predicted by NDVI that ranged between the middle range of 0.5 and 0.7. Brodrick et al. (2017) evaluated NDVI values associated with tree mortality and noted ranges in variability for NDVI values that correspond to combinations of live and dead vegetation conditions and align with our findings. The time series analysis shows a decline in mean annual NDMI values that corresponds to changes in vegetation conditions associated with MPB outbreaks. The time series parallels trends seen in other forests affected by MPB outbreaks in western North America (Goodwin et al. 2008, Meigs et al. 2011). Change between pre-outbreak conditions and red-phase outbreak conditions indicate that most areas across the landscape experience changes in NDMI values associated with tree mortality from MPB attack (Goodwin et al. 2008). This finding supports the development and use of Landsat-derived outbreak severity to assess MPB outbreak dynamics and as an explanatory variable in our BRT models.

Characteristics and drivers of high burn severity

High burn severity covers large portions within the fire perimeters of our study landscape and is characteristic of the infrequent high-severity fire regimes of the region; however, we also observed substantial areas burning at lower severity. Our results offer a contemporary perspective of burn mosaics for this region without the influence of active forest management (e.g., harvest, suppression), due to the wilderness context. Landscapes included between 18% and 43% forested area burning at lower severity (e.g., not high severity) and included fire refugia, here unburned areas that with either live canopies or legacies of MPB outbreaks. While we have split burn severity into classes for interpretability, we recognize that postfire landscapes are characterized by gradients composed of ecological and structural legacies that influence ecosystem response to disturbances. For these landscapes, postfire burn mosaics include gradients of lower severity and fire refugia as well as moderate to high severity that are characterized a combination of standing and downed snags, snags with deep char, both even- and mixed-aged cohorts of lodgepole pine seedling at variable densities, and early seral species and postfire specialists (Talucci and Krawchuk 2019, Talucci et al. 2019 [This dissertation, Chapter 3]). Previous work in BC on fire dynamics in lodgepole pine forest has been limited and focused on surrounding regions that have characterized fire regimes from historical reconstructions of age classes that have indicated wide ranges of variability in terms of fire return that are dependent on moisture gradients and forest composition (Delong 1998, Steventon 2001, Francis et al. 2002). In this region, area burned has shown increases of 2.4% per year from 1984 to 2015 (Coops et al. 2018). The extent of the MPB outbreak, in combination with continued increases in area burned, will result in fires burning through mixtures of live and dead fuels that can support high burn severity across large portions of the landscape.

Across the forested landscapes of our study area, the mixture of live and dead fuels that contained the legacy of MPB outbreaks (i.e. prefire vegetation conditions) had the greatest probability of burning at high severity. In both the moderate-FWI and high-FWI models, the non-linear relationship between high burn severity and NDVI (prefire vegetation conditions) manifests as a ‘hump shape’ in the partial-dependence plots in the BRT analyses. This result suggests that the greatest probability of high burn severity occurs between NDVI values from ~0.5 to ~0.7, which corresponds to a mixture of live and dead vegetation. The data distribution for sampling was dominated by NDVI values between 0.5-0.7, a range associated with higher probability of high burn severity. As such, we find that prefire vegetation conditions (i.e. live and dead fuels) are an important contributor to high burn severity (Krawchuk et al. 2006), but also quantify an increase in high severity burning as an outcome of moderate prefire mortality from MPB outbreak after accounting for fire weather. Fuel structure exerted more influence on high burn severity under moderate fire weather conditions in comparison to high fire weather conditions, which points to the importance of fuels during more moderate burning conditions (Talucci and Krawchuk 2019). Previous work had not identified a signal from fuel structures associated with MPB outbreaks and had been limited in scope to extreme fire years (Hart et al. 2015) or evaluations at the scale of the fire event (Meigs et al. 2016), which both limits interpretability of these relationships and does not account for the full range of variability in the fire environment – i.e. fuels, weather, and topography.

Our results suggest that although outbreak severity conditions are important to consider, prefire vegetation conditions that integrate the legacy of outbreak and post-outbreak ecological succession provided more explanatory power for areas that experienced high burn severity here. The influence of outbreak severity, as measured by dNDMI values, varied between models with a greater influence in the high-FWI model and a lower influence in the moderate-FWI model. In both models, a greater change in dNDMI corresponded with higher probabilities of high burn severity. The dNDMI was not strongly correlated with NDVI, but both indicated losses in live tree canopies and mixtures of live and dead fuels. Fires burned approximately a decade after the red phase of the outbreak, and stand breakdown – i.e. needle loss, branch breakage, and tree fall, likely continued to alter the configuration of live and dead fuels up until the fire event (Talucci et al. 2019 [This dissertation, Chapter 3]). Therefore, the snapshot captured during the red phase of the outbreaks is not fully indicative of what burned a decade later. Moreover, the legacy from the outbreaks and successional processes that ensue in conjunction with stand degradation is partially captured by the prefire vegetation conditions. Importantly in these sub-boreal landscapes, outbreaks have left a legacy of deadwood that is integral to the composition and structure of the forest. This combination of live and dead fuel complexes is a legacy that spans much of BC's central interior that experienced record area burned during the 2017 and 2018 fire seasons, further underscoring the importance of outbreak legacies on burn severity for these landscapes.

Fire weather conditions were an important variable of influence in both models either ranking first or second for high- and moderate-FWI models respectively. The relationships were generally a direct positive relationship, with some variability in the partial-dependence plots influenced by the distribution and range of the data (Figure 4.A4). In sub-boreal forests, fire regimes are typically dependent on synoptic climate conditions, high-pressure systems that generate hot and dry summer conditions that reduce fuel moisture and generate settings conducive for carrying wildfire (Nash and Johnson 1996). Our models show the influence of daily fire weather on the probability of high burn severity for a pixel, even once data have been binned into categories of moderate and high fire weather. Generally, whether under moderate or high fire weather conditions, our models indicate a greater (>50%) probability of high burn severity overall. For the fires in this study, there were only a few days where weather conditions were benign, indicating that climate conditions conducive to moderate and high fire weather conditions were widespread throughout each fire's duration. Due the wilderness management objectives for these provincial parks, all fires burned under modified response (i.e. minimal suppression), producing a fire mosaic with burn severity generated from days of high fire weather as well as moderate burning conditions. Typically, suppression operations take advantage of moderate weather conditions to stop or alter the natural disturbance process (Finney et al. 2009), which did not happen on these landscapes. In addition, all three fire years were drier than climate normals (Figure 4.A1), indicating baseline conditions conducive for large fires. In both models, no single variable held a majority of influence indicating that it is the combination of all variables that contribute to high burn severity, which corresponds to the fire behavior triangle (Countryman 1972) and resonates with research on environmental and climatic gradients (Parisien and Moritz 2009, Krawchuk and Moritz 2011, Whitman et al. 2015). Elevation ranked third or fourth in variable importance for the moderate and high models respectively, indicating the limited influence of topography on the flat to gently rolling terrain that typifies this landscape.

Caveats

Satellite-based remote sensing evaluations provide opportunities for landscape-scale assessments but are conducted at coarser resolution than field-based measures. These landscape-scale assessments are particularly useful in remote wilderness settings where field sampling can be limited and opportunistic. Research continues to evaluate how spectral indices from satellite data relate to field measures in order to better link spectral data to environmental conditions (McCarley et al. 2017, Whitman et al. 2018, Harvey et al. 2019). The coarse resolution, top-down view, and the imperfect accuracy of linking a field observation to the corresponding pixel in a satellite image limits how closely spectral data are associated with environmental conditions (Meigs et al. 2011). We suggest that field- and satellite-based methods are complementary approaches with distinct advantages and disadvantages, and we demonstrate this complementarity by integrating Landsat, fine resolution aerial imagery, and field observations. While we were not specifically aiming to say that a specific spectral value corresponds to a specific amount of outbreak mortality or fuel type, our evaluation and development of spatial data for analysis indicates that gradients of spectral values correspond to finer resolution gradients of forest composition and structure (e.g. live/dead, sparse/dense vegetation) based on aerial imagery, which are useful for understanding relationships between disturbances. Field and satellite data both capture information for a specific location at a specific moment in time, and the collection timing of these two types of data rarely align temporally, which can limit the link between image-derived spectra and environmental conditions. While we used field data from 2013 to inform breaks in RdNBR values, field data collected two to four years postfire did not correspond to clear breaks due to changes in environmental conditions that include early successional regrowth. For forests with substantial tree mortality, structure and composition continues to change over time as stands break down and recover, which could limit the inference between a field observation from a specific moment in time that does not temporally align with the satellite observation. Additionally, the fire weather data index we used (FWI) is a daily measurement from local weather stations that includes lag calculations that account for weather conditions for the entire season. The FWI is the best metric available but does not necessarily capture the spatiotemporal variability in precipitation, wind conditions, and actual conditions on the ground when a given pixels burns (Wagenbrenner et al. 2016), or the localized weather features that fires can generate (Potter 2012).

Conclusion

This study quantifies important drivers of high burn severity for sub-boreal forests that have experienced widespread effects of MPB outbreaks prior to wildfires. We provide key insights to burn severity characteristics at landscape scales for large fires that burned unhindered by suppression. High burn severity covered large portions of the burn mosaic and was influenced by prefire vegetation conditions, including the legacy of MPB outbreak. The mixture of live and dead trees due to MPB outbreaks was associated with the highest probability of high burn severity for fires burning through post-outbreak gray-phase conditions. This suggests that the legacy of MPB outbreaks can influence the probability of high burn severity across these landscapes, after accounting for weather and topography. In addition, our study illustrates that fire weather associated with synoptic climate conditions prime the landscape for large, severe wildfire events. This relationship is pertinent under current and future climate projections. In the long-term, high burn severity could influence future forest resilience when disturbances recur in short intervals.

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Literature Cited

Abatzoglou, J. T., S. Z. Dobrowski, S. A. Parks, and K. C. Hegewisch. 2018. Terraclimate, a high-resolution global dataset of monthly climate and climate water balance from 1958-2015. Scientific Data.

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

Alexander, M. E., and W. J. De Groot. 1988. Fire Behavior in Jack Pine Stands as related to the Canadian Forest Fire Weather Index (FWI) System. Canadian Forestry Service, Northwest Region, Edmonton, Alberta, Canada.

Axelson, J. N., R. I. Alfaro, and B. C. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. Forest Ecology and Management 257:1874–1882.

BCMFLNRO. 2012. Vegetation Resources Inventory. British Columbia Ministry of Forests Lands and Natural Resource Operations, Victoria, BC, Canada.

BCMFLNRO. 2016. Aerial Overview Survey Data Files. https://www2.gov.bc.ca/gov/content/environment/research-monitoring-reporting/monitoring/aerial-overview-surveys/data-files.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Notes and observations: Aspect transformation in site productivity research. Journal of Forestry 64:691–692.

Bessie, W. C., and E. A. Johnson. 1995. The Relative Importance of Fuels and Weather on Fire Behavior in Subalpine Forests. Ecology 76:747–762.

Brodrick, P. G., G. P. Asner, and P. G. Brodrick. 2017. Remotely Sensed Predictors of Conifer Tree Mortality During Severe Drought. Environmental Research Letters 12:1–9.

Cartwright, J. 2018. Landscape topoedaphic features create refugia from drought and insect disturbance in a lodgepole and whitebark pine forest. Forests 9:715.

Cichowski, D., and D. Morgan. 2009. Tweedsmuir-Entiako Caribou Population: Summary of Ecology and Effects of Disturbance. Smithers, BC.

Coops, N. C., T. Hermosilla, M. A. Wulder, J. C. White, and D. K. Bolton. 2018. A thirty year, fine-scale, characterization of area burned in Canadian forests shows evidence of regionally increasing trends in the last decade. PLoS ONE 13:1–19.

Countryman, C. M. 1972. The fire environment concept. Berkeley, CA.

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

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192.

Delong, S. C. 1998. Natural Disturbance Rate and Patch Size Distribution of Forests in Northern British Columbia : lmplications for Forest Management 72.

Dillon, G. K., Z. A. Holden, P. Morgan, M. A. Crimmins, E. K. Heyerdahl, and C. H. Luce. 2011. Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. Ecosphere 2:1–33.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. The Journal of animal ecology 77:802–13.

Finney, M., I. C. Grenfell, and C. W. McHugh. 2009. Modeling containment of large wildfires using generalized linear mixed-model analysis. Forest Science 55:249–255.

Francis, S. R., S. Skinner, M. Gallagher, and C. Marion. 2002. Characterising fire regimes: Fire history research in the SBPS and SBS biogeoclimatic zones of the Cariboo Forest Region. Williams Lake, British Columbia, British Columbia.

Friedman, J. 2001. Greedy Function Approximation : A Gradient Boosting Machine. The Annals of Statistics 29:1189–1232.

GeoBC. 2012. 2012 Digital Air Photos of B.C. GeoBC, Vancover, BC.

Goodwin, N. R., N. C. Coops, M. A. Wulder, S. Gillanders, T. A. Schroeder, and T. Nelson. 2008. Estimation of insect infestation dynamics using a temporal sequence of Landsat data. Remote Sensing of Environment 112:3680–3689.

Hart, S. J., T. Schoennagel, T. T. Veblen, and T. B. Chapman. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proceedings of the National Academy of Sciences of the United States of America 112:4375–80.

Harvey, B. J., R. A. Andrus, and S. C. Anderson. 2019. Incorporating biophysical gradients and uncertainty into burn severity maps in a temperate fire-prone forested region. Ecosphere 10:1–20.

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecological Applications 24:1608–1625.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proceedings of the National Academy of Sciences 111:15120–15125.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984-2010). Landscape Ecology 31:2367–2383.

Hermosilla, T., M. A. Wulder, J. C. White, N. C. Coops, and G. W. Hobart. 2015. An integrated Landsat time series protocol for change detection and generation of annual gap-free surface reflectance composites. Remote Sensing of Environment 158:220–234.

Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2016. dismo: species distribution modeling. R Package version 1.0-1.15.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367–368.

Hopkins, A. D. 1909. Practical information on the Scolytid beetles of North American forests. Page Barkbeetles of the genus Dendroctonous. Washington, DC.

Hunt, E. R., B. N. Rock, and P. S. Nobel. 1987. Measurement of leaf relative water content by infrared reflectance. Remote Sensing of Environment 22:429–435.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Kennedy, R. E., Z. Yang, and W. B. Cohen. 2010. Remote Sensing of Environment Detecting trends in forest disturbance and recovery using yearly Landsat time series : 1 . LandTrendr — Temporal segmentation algorithms. Remote Sensing of Environment 114:2897–2910.

Kennedy, R. E., Z. Yang, W. B. Cohen, E. Pfaff, J. Braaten, and P. Nelson. 2012. Spatial and temporal patterns of forest disturbance and regrowth within the area of the Northwest Forest Plan. Remote Sensing of Environment 122:117–133.

Kennedy, R. E., Z. Yang, N. Gorelick, J. Braaten, L. Cavalcante, W. Cohen, and S. Healey. 2018. Implementation of the LandTrendr Algorithm on Google Earth Engine. Remote Sensing 10:691.

Key, C. H., and N. C. Benson. 2006. Landscape assessment (LA): Sampling and analysis methods. USDA Forest Service General Technical Report RMS-GTR-164-CD:1–55.

Kincaid, T. M., and A. R. Olsen. 2017. spsurvey: Spatial Survey Design and Analysis. R Packages version 3.4.

Kolden, C. A., J. A. Lutz, C. H. Key, J. T. Kane, and J. W. Van Wagtendonk. 2012. Mapped versus actual burned area within wildfire perimeters : Characterizing the unburned. Forest Ecology and Management:38–47.

Krawchuk, A. M. A., S. G. Cumming, M. D. Flannigan, and R. W. Wein. 2006. Biotic and Abiotic Regulation of Lightning Fire Initiation in the Mixedwood Boreal Forest. Ecology 87:458–468.

Krawchuk, M. A., S. L. Haire, J. Coop, M. A. Parisien, E. Whitman, G. Chong, and C. Miller. 2016. Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. Ecosphere 7.

Krawchuk, M. A., and M. A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. Ecology 92:121–132.

Macias Fauria, M., and E. A. Johnson. 2008. Climate and wildfires in the North American boreal forest. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2317–2329.

McCarley, T. R., C. A. Kolden, N. M. Vaillant, A. T. Hudak, A. M. S. Smith, B. M. Wing, B. S. Kellogg, and J. Kreitler. 2017. Multi-temporal LiDAR and Landsat quantification of fire-induced changes to forest structure. Remote Sensing of Environment 191:419–432.

Meigs, G. W., J. L. Campbell, H. S. J. Zald, J. D. Bailey, D. C. Shaw, and R. E. Kennedy. 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? 6:118.

Meigs, G. W., R. E. Kennedy, and W. B. Cohen. 2011. A Landsat time series approach to characterize bark beetle and defoliator impacts on tree mortality and surface fuels in conifer forests. Remote Sensing of Environment 115:3707–3718.

Meigs, G. W., H. S. J. Zald, J. L. Campbell, W. S. Keeton, and R. E. Kennedy. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environmental Research Letters 11.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.

Nash, C. H., and E. A. Johnson. 1996. Synoptic climatology of lightning-caused forest fires in subalpine and boreal forests. Canadian Journal of Forest Research 26:1859–1874.

Parisien, M.-A., and M. A. Moritz. 2009. Environmental controls on the distribution of wildfire at multiple spatial scales. Ecological Monographs 79:127–154.

Parks, S. A. 2014. Mapping day-of-burning with coarse-resolution satellite fire-detection data. International Journal of Wildland Fire 23:215.

Parks, S. A., L. M. Holsinger, M. H. Panunto, W. M. Jolly, S. Z. Dobrowski, and G. K. Dillon. 2018. High-severity fire: Evaluating its key drivers and mapping its probability across western US forests. Environmental Research Letters 13.

Parminter, J. 1992. Typical historic patterns of wildfire disturbance by biogeoclimatic zone. Minsitry of Forests, Victoria, British Columbia, Canada.

Perrakis, D. D. B., R. a. Lanoville, S. W. Taylor, and D. Hicks. 2014. Modeling Wildfire Spread in Mountain Pine Beetle-Affected Forest Stands, British Columbia, Canada. Fire Ecology 10:10–35.

Potter, B. E. 2012. Atmospheric interactions with wildland fire behaviour - II. Plume and vortex dynamics. International Journal of Wildland Fire 21:802.

R Development Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. a. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. BioScience 58:501.

Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985-2010). Ecosphere 8:e01695.

Ridgeway, G. 2015. gbm: generalized boosted regression models. R package version 1.3-5.

Roy, D. P., V. Kovalskyy, H. K. Zhang, E. F. Vermote, L. Yan, S. S. Kumar, and A. Egorov. 2016. Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. Remote Sensing of Environment 185:57–70.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. BioScience 54:661–676.

Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.

Steventon, J. D. 2001. Morice Timber Supply Area Timber Supply Review. Smithers, British Columbia, British Columbia.

Talucci, A. C., and M. A. Krawchuk. (2019). Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. Ecosphere 10(5):e02744. 10.1002/ecs2.2744

Talucci, A. C., K. P. Lertzman, and M. A. Krawchuk. (2019). Drivers of lodgepole pine recruitment across a gradient of bark beetle outbreaks and wildfire in British Columbia. Forest Ecology and Management, *in review*. [This dissertation, Chapter 3]

Talucci, A. C. (2019). Data and Code: Beetles and fire landscape-scale BC (Version v0.1) [Data set]. Zenodo. http://doi.org/10.5281/zenodo.3235811

VanDerWal, J., L. Falconi, S. Januchowski, L. Shoo, and C. Storlie. 2014. SDMTools: Species Distribution Modelling Tools: Tools for processing data associated with species distribution modeling exercises. R Packages version 3.4.

Wagenbrenner, N. S., J. M. Forthofer, B. K. Lamb, K. S. Shannon, and B. W. Butler. 2016. Downscaling surface wind predictions from numerical weather prediction models in complex terrain with WindNinja. Atmospheric Chemistry and Physics 16:5229–5241.

Van Wagner, C. E. 1987. Development and structure of the Canadian forest fire weather index system. Page Forestry Technical Report 35. Ottawa.

Walter, J. A., and R. V. Platt. 2013. Multi-temporal analysis reveals that predictors of mountain pine beetle infestation change during outbreak cycles. Forest Ecology and Management 302:308–318.

Wang, T., A. Hamann, D. L. Spittlehouse, and T. Q. Murdock. 2012. ClimateWNA—High-resolution spatial climate data for western North America. Journal of Applied Meteorology and Climatology 51:16–29.

Whitman, E., E. Batllori, M.-A. Parisien, C. Miller, J. D. Coop, M. A. Krawchuk, G. W. Chong, and S. L. Haire. 2015. The climate space of fire regimes in north-western North America. Journal of Biogeography 42:1736–1749.

Whitman, E., M.-A. Parisien, D. K. Thompson, R. J. Hall, R. S. Skakun, and M. D. Flannigan. 2018. Variability and drivers of burn severity in the northwestern Canadian boreal forest. Ecosphere 9.

Wulder, M. A., J. C. White, D. Grills, T. Nelson, and N. C. Coops. 2009. Aerial overview survey of the mountain pine beetle epidemic in British Columbia: Communication of impacts. BC Journal of Ecosystems and Management 10:45–58.

Tables

Table 4.1. Explanatory and response variables and descriptions that were considered for BRT models. From each group, the variable with the most explanatory power was selected for inclusion in the two final models (variables in *italics*).

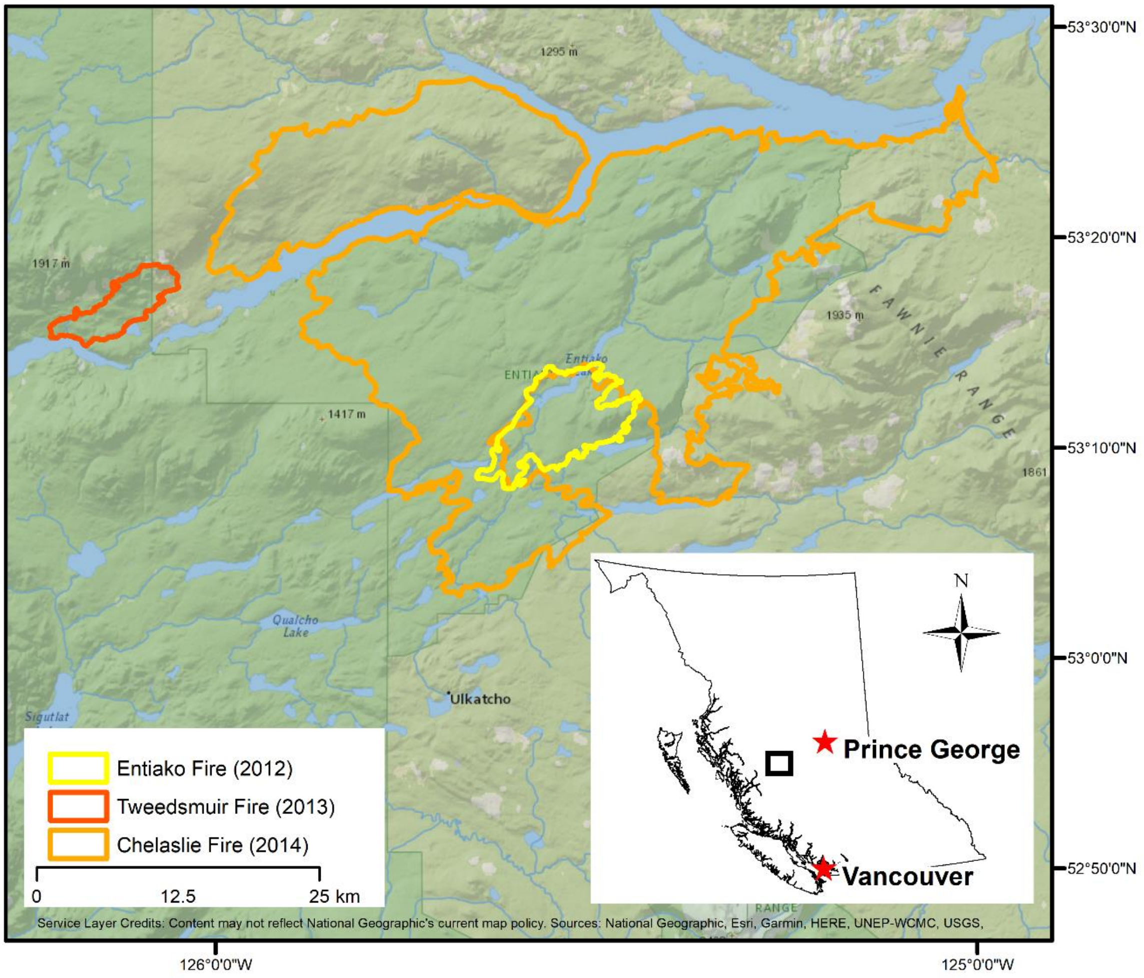
Variable	Index	Description of index	Source
Burn Severity	RdNBR	Relative differenced Normalized Burn Ratio. Calculated from pre and post fire Normalized Burn Ratio (NBR) as (NIR-SWIR2)/(NIR+SWIR2). RdNBR relies on the differenced Normalized Burn Ration (dNBR) calculated as: dNBR=prefire NBR-postfire NBR and then RdNBR is calculated as: $RdNBR = dNBR/\sqrt{ABS(prefireNBR/1000)}$	(Miller and Thode 2007)
Outbreak severity conditions	*dNDMI*	Normalized difference moisture index. Calculated mean value to generate a composite image from the red phase of the MPB outbreak. NDMI is calculated as: NDMI=(NIR-SWIR1)/(NIR+SWIR1) and dNDMI is calculated as: dNDMI=*pre-outbreak* NDMI (1995)-*post-outbreak* NDMI (2006)	(Hunt et al. 1987, Goodwin et al. 2008, Walter and Platt 2013)
Prefire vegetation conditions	NDMI	Normalized difference moisture index. Calculated using prefire imagery, one year prior to fire event	(Hunt et al. 1987, Goodwin et al. 2008, Walter and Platt 2013)
	NDVI	Normalized difference vegetation index. Calculated using prefire imagery	
	EVI	Enhanced vegetation index. Calculated using prefire imagery. EVI=2.5×(NIR-RED)/(NIR+6×RED-7.5×BLUE+1)	
Topography	ASPTR	Aspect transformation in site productivity research (ASPTR) is the azimuth transformed from degrees to a range from 0 to 2	(Beers et al. 1966)
	TPI (450m)	Difference among a pixel's elevation and the mean elevation from the surrounding neighborhood of pixels within 450m	
	Percent slope	Estimated percent slope for each pixel	

	Elevation	Elevation above sea level in meters	
Fire Weather	*FWI*	Fire Weather Index. Calculated from several weather variables across the entire fire season from the nearest weather station and assigned to pixels based on day-of-burn using MODIS hotspot data	(Alexander and De Groot 1988)

Table 4.2. Summary of BRT model fit for two models: the probability of high burn severity under moderate and high fire weather conditions. The relative influence of each explanatory variable in the model is shown with ranked order.

		Model Moderate Fire Weather	Model High Fire Weather
Model Fit	Sample size (n)	31977	28823
	Sample size presence/absence	22,236/9,741	21,305/7,518
	Percent of total sample points	52.6%	47.4%
	Number of BRT Trees	11,200	11,050
	Percent Deviance Explained	0.14	0.18
	AUROC	0.73	0.77
	Cross-validation mean deviance	1.08	0.96
	Cross-validation mean correlation	0.39	0.43
	Cross-validation ROC	0.74	0.77
Relative influence of explanatory variables	NDVI prefire (rank)	37.4% (1)	27.8% (2)
	FWI (rank)	27.4% (2)	36.4% (1)
	Elevation (rank)	23.2% (3)	13.9% (4)
	dNDMI beetle (rank)	12.0% (4)	21.9% (3)

Figures



Service Layer Credits: Content may not reflect National Geographic's current map policy. Sources: National Geographic, Esri, Garmin, HERE, UNEP-WCMC, USGS,

Figure 4.1. Location of study area. Fire perimeters are situated within Entiako and Tweedsmuir Provincial parks (darker green background color). Inset map shows the location of the study area, as a black box, within the central interior of the province of British Columbia, Canada.

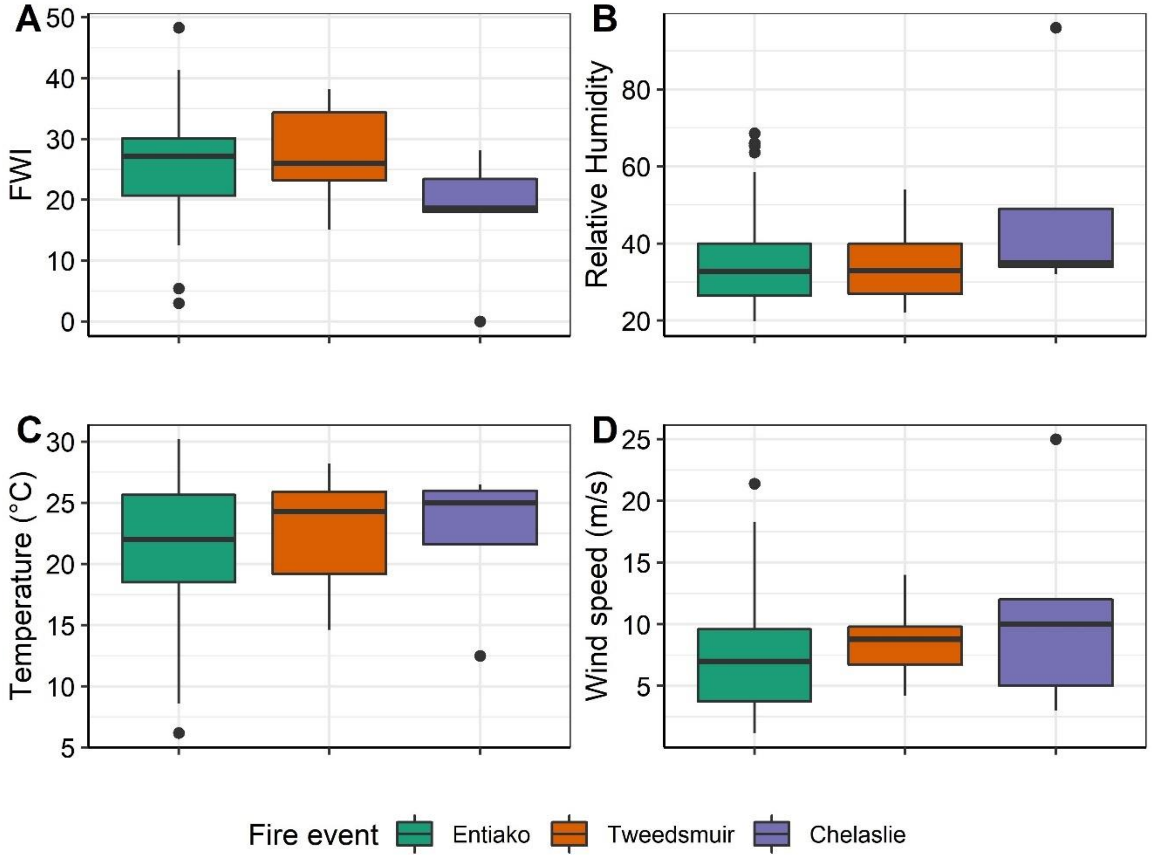


Figure 4.2. Fire weather conditions across wildfire events. All fires experienced a range of moderate to high fire weather throughout the burning period, as estimated by the Fire Weather Index (FWI): moderate FWI >13-29 and high >29 (**A**). All fires appear relatively similar for the ranges of relative humidity (**B**), temperature (**C**), and wind speeds (**D**).

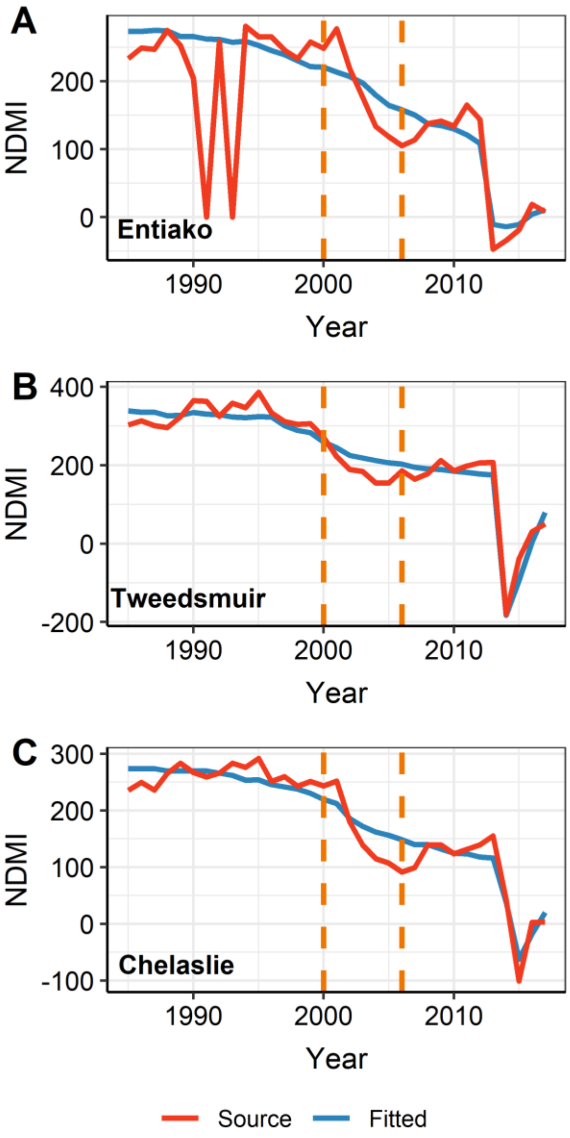


Figure 4.3. The spectral trajectory of NDMI over time. Each panel highlights declines in NDMI values associated with MPB outbreaks for a given fire: Entiako (R10171) burned in 2012 (A), Tweedsmuir (R10252) burned in 2013 (B), and Chelaslie (R10070) burned in 2014 (C). Declines in NDMI spectral values occur over the duration of the outbreaks. The orange-dashed lines bracket the timeframe used to measure outbreak severity, 2000-2006. The red-line shows the sourced data, mean NDMI value from sampled pixels per year. The blue line indicated the fitted values calculated by the segmentation algorithm from LandTrendr and based on the sourced values in the red line. The big ‘W’ pattern in the sourced data for Entiako (A) indicates two dates with missing data or data masked by clouds.

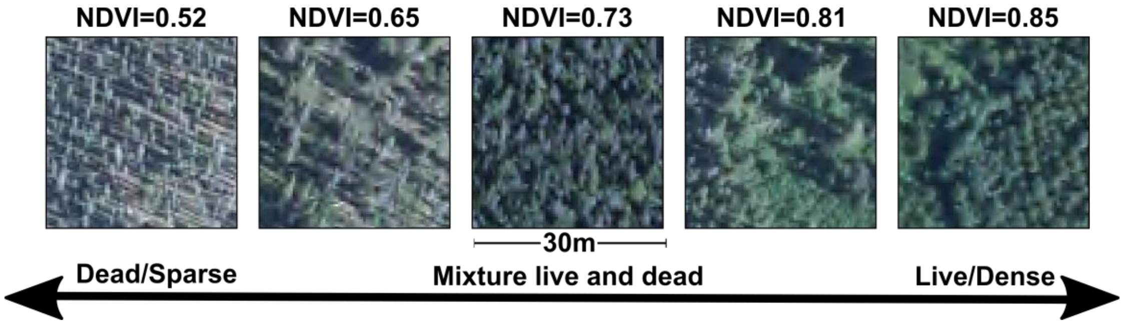


Figure 4.4. Examples of prefire vegetation conditions from high-resolution aerial imagery (2012). Imagery was used to assess and interpret prefire vegetation conditions (NDVI) and outbreak severity conditions (NDMI) across a gradient of spectral indices that corresponded to gradients of forest composition and structure. Sample images here are equivalent to 30m, matching the resolution of Landsat pixels. The examples here came from a random sample of points (n=150) from the full sample (n=60,800). Images show a gradient of dead/sparse forest vegetation to a mixture of live and dead forest vegetation to live/dense forest vegetation that correspond to increases in NDMI and NDVI values from left to right.

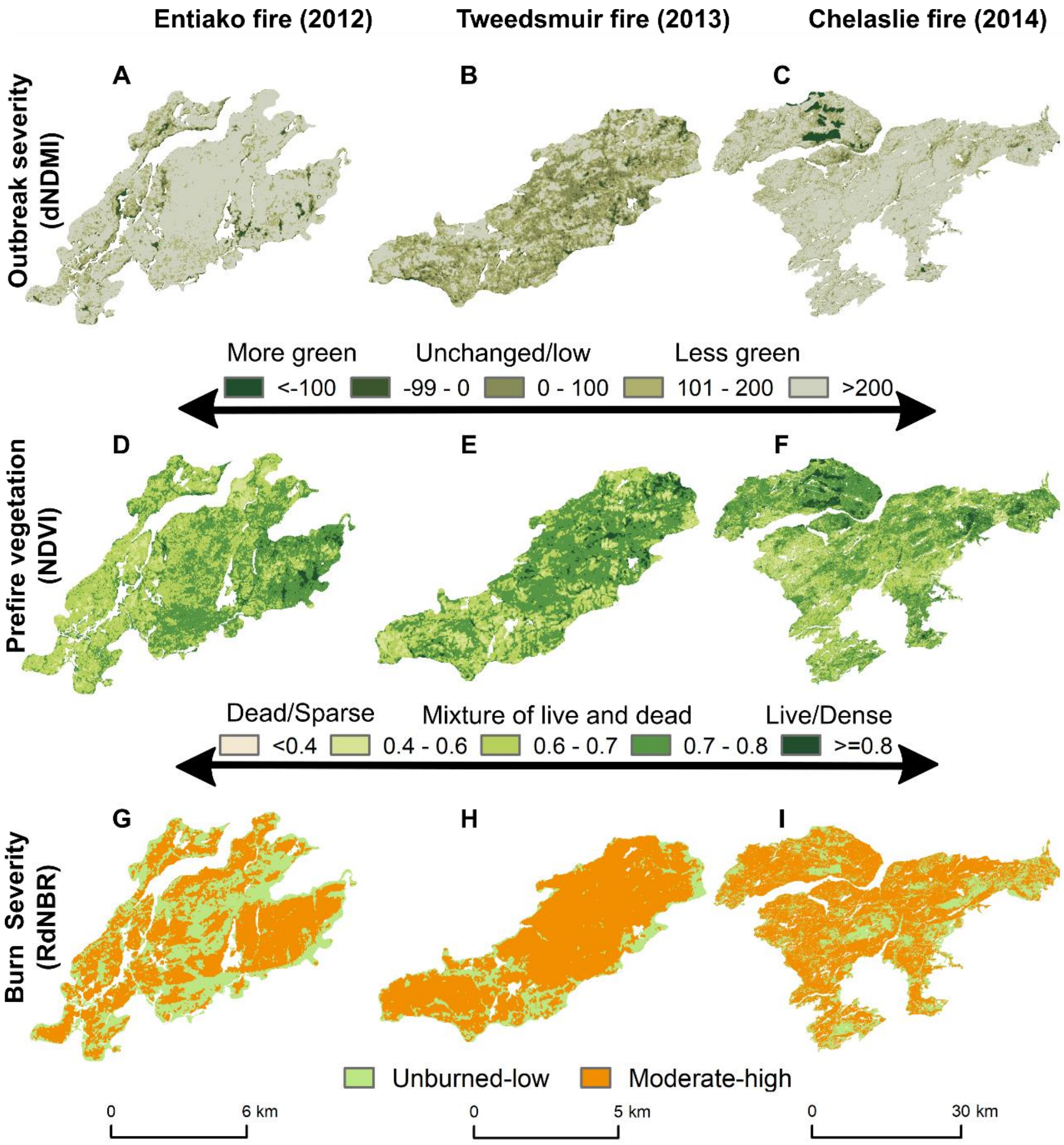


Figure 4.5. Spatial data layers for prefire vegetation, outbreak severity, and burn severity for each fire perimeter. Outbreak severity and prefire vegetation are gradients of composition and structure with variable levels of live and dead, trees and shrubs, dense and spare tree vegetation. See Figure 4.4 for images associated with these gradients. Outbreak severity are represented by NDMI (A-C). Prefire vegetation conditions are characterized by NDVI (D-F). Burn severity is illustrated with RdNBR and was split into a binary response variable of presence/absence of moderate-high (RdNBR ≥ 600) and unchanged to low (RdNBR < 600) burn severity. (G-I).

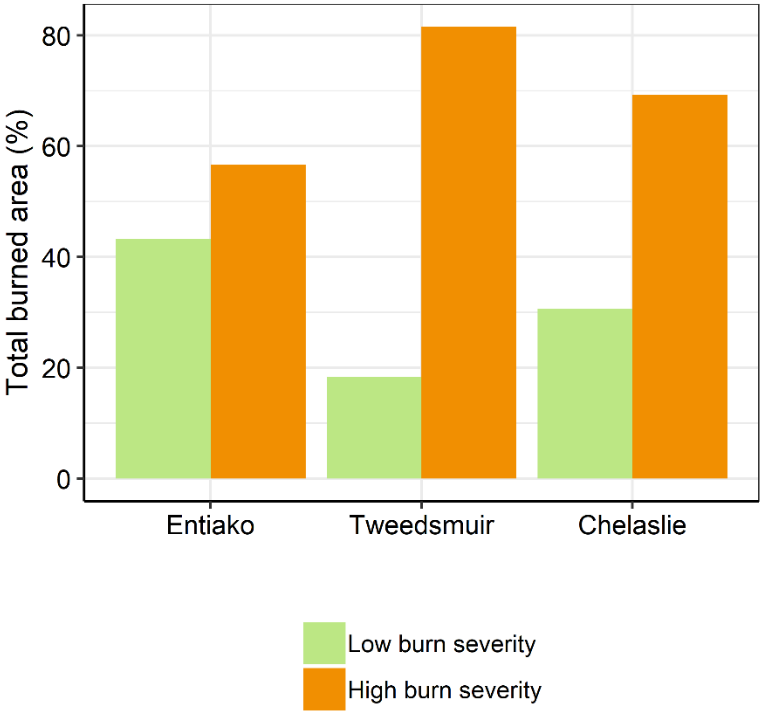


Figure 4.6. Percent of burned area by burn severity classes. High burn severity is RdNBR ≥ 600 and low burn severity is RdNBR < 600. Percent area burn are specific to each fire – Entiako (R10171) and burned in 2012, Tweedsmuir (R10252) and burned in 2013, and Chelaslie (R10070) and burned in 2104.

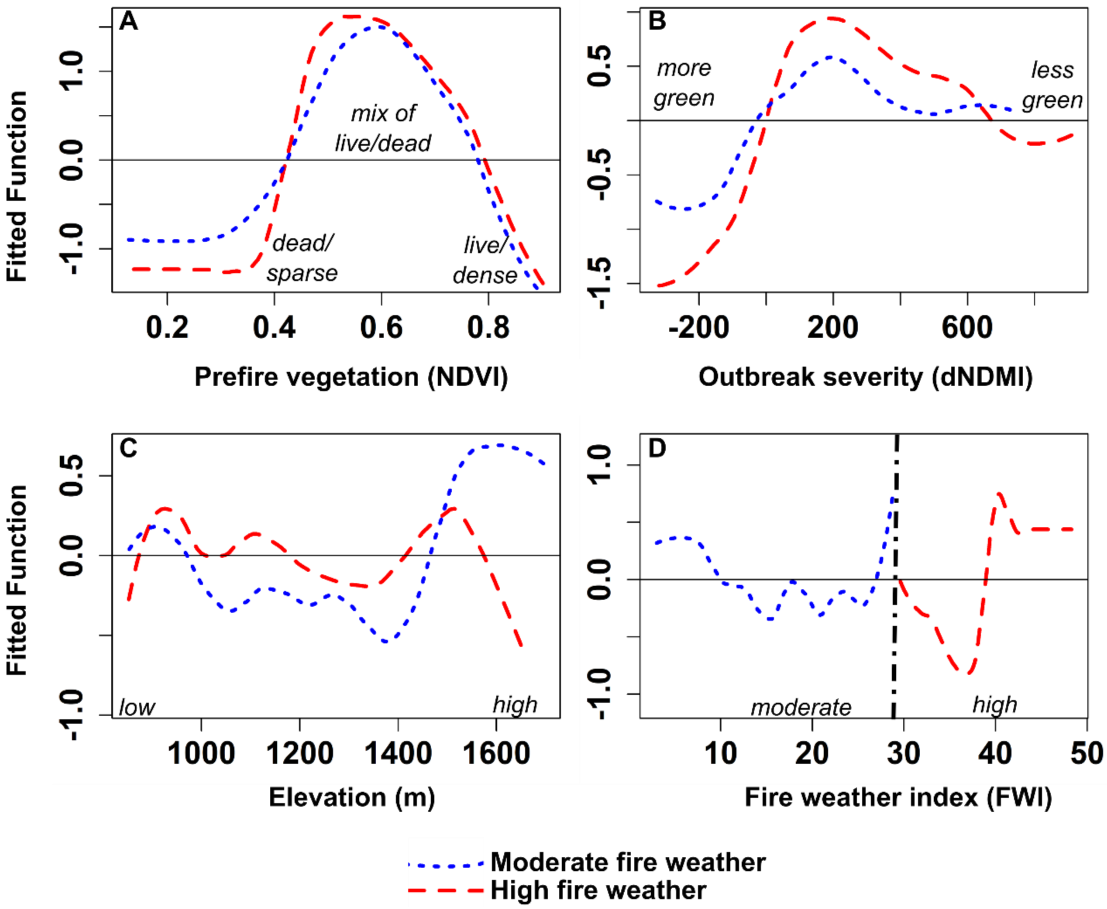


Figure 4.7. Drivers of high burn severity from each variable group (Table 4.1). Partial dependence plots show the relationships between explanatory variables and the probability of high burn severity while accounting for interactions among variables in BRT models. Note that panel D shows fire weather, which is split by the black dot-dashed line indicating the two models, moderate fire weather and high fire weather. Therefore, there is no overlap between the trend lines and the break between the lines is a function of splitting the models by fire weather. See appendix figure 4.A4 for the distribution of the data for each of these explanatory variables.

Appendix

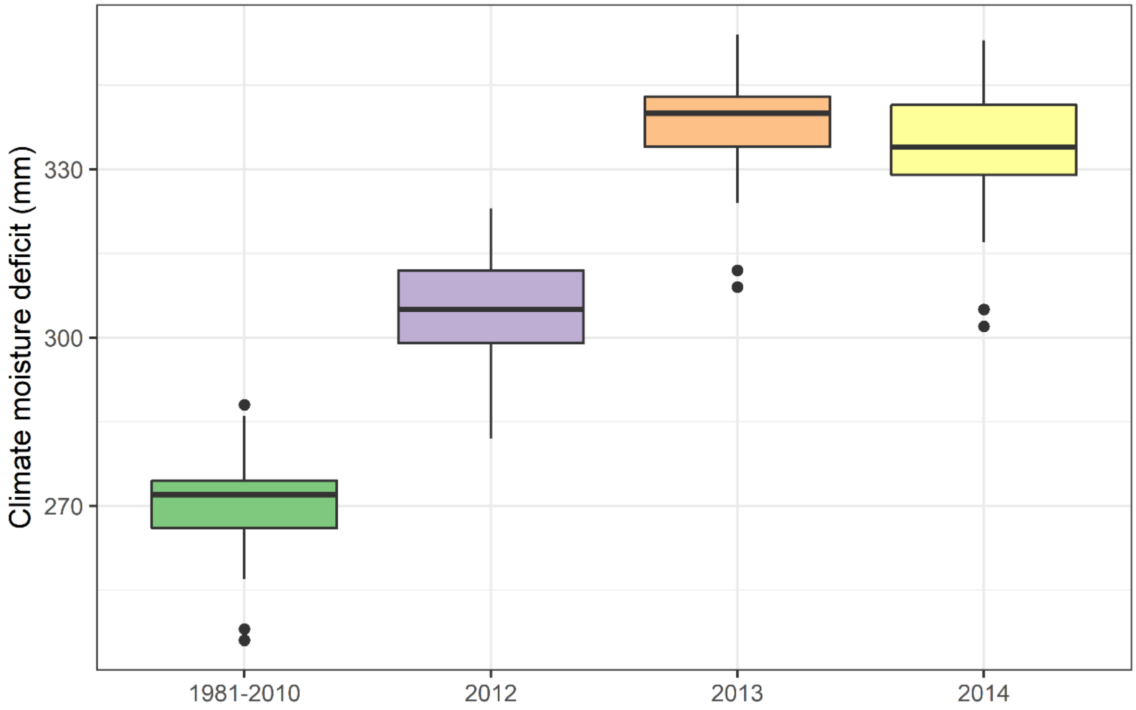


Figure 4.A1. Climate moisture deficits for fire years and climate normal. Fire years 2012, 2013, 2014 all experienced greater climate moisture deficits in comparison to climate normal data for 1981-2010.

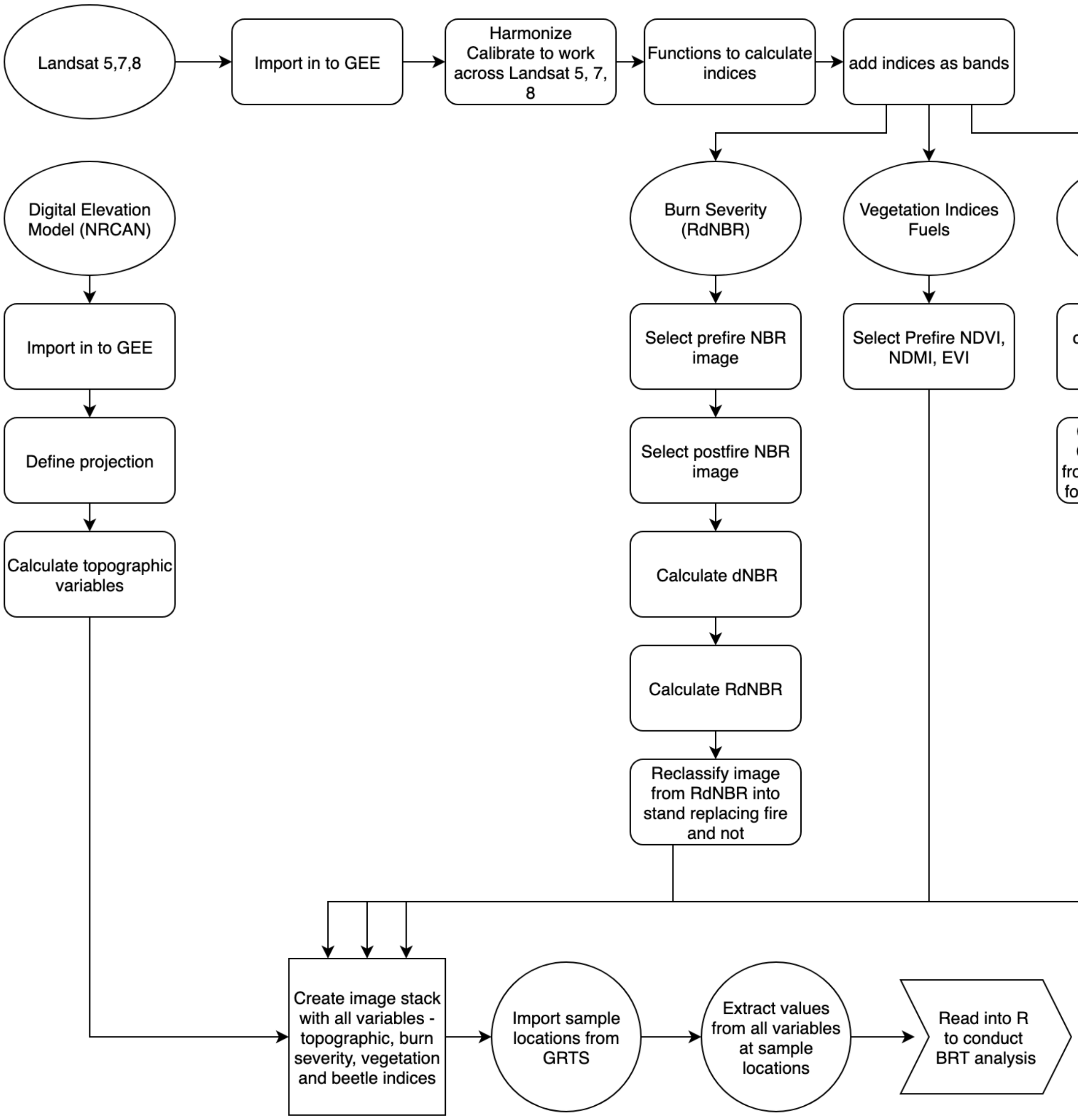


Figure 4.A2. Work flow for Google Earth Engine and spatial data development.

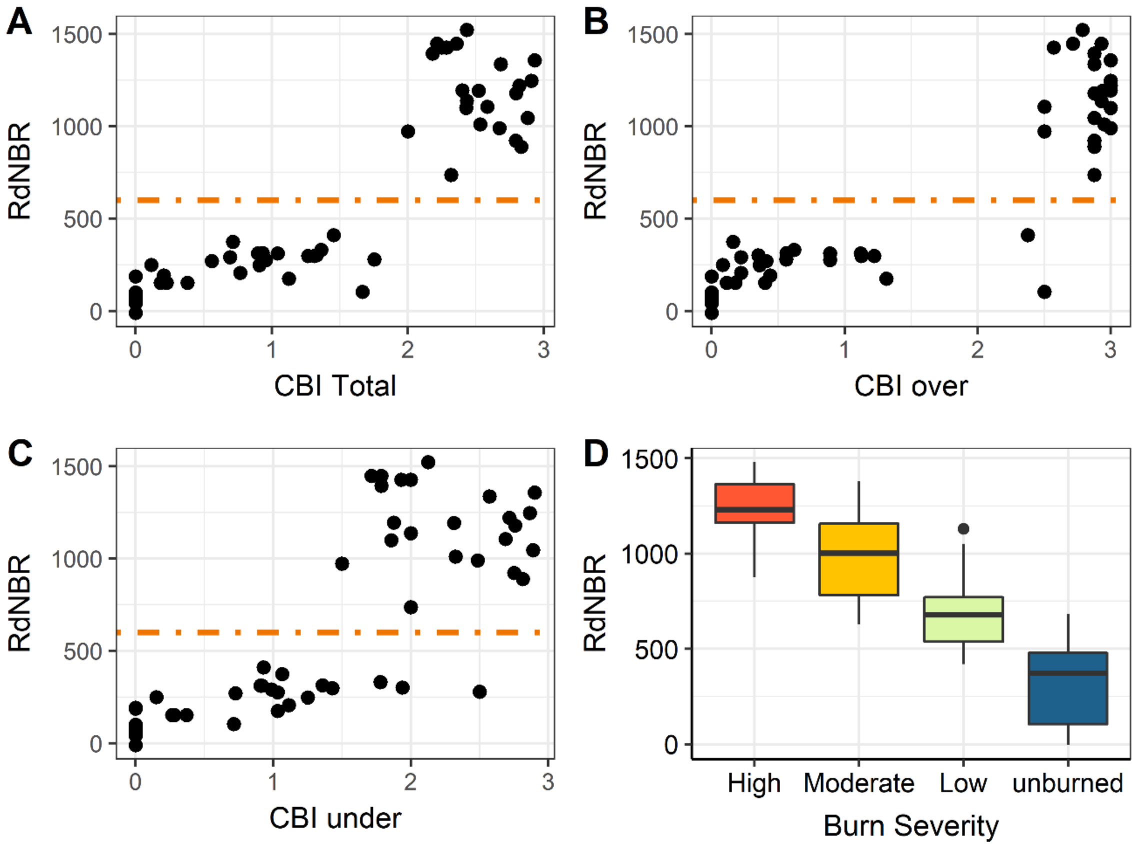


Figure 4.A3. Comparison between field data and RdNBR values. Panels A-C include field data measured as the composition burn index (CBI) data for the Entiako Fire plotted against RdNBR values, collected separately by Krawchuk in 2013 one-year post fire. The orange, dot-dashed line indicated the break point for high burn severity (RdNBR >600). Panel D includes field data measured and classified across all fires two to four years post fire (Talucci et al. 2019 [This dissertation, Chapter 3]).

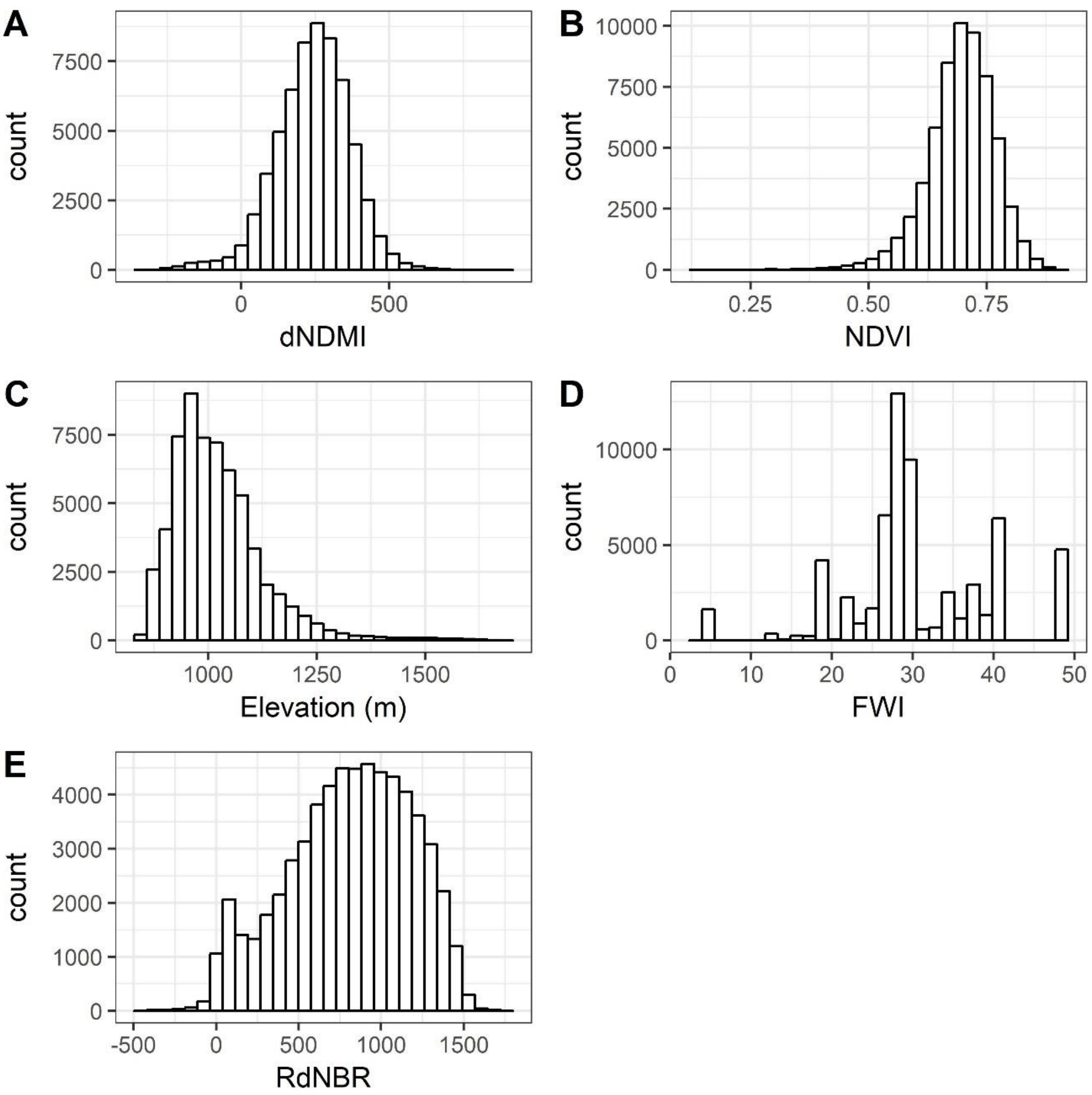


Figure 4.A4. Histograms of satellite derived data across all sample plot locations (*n* = 60,800): NDMI (outbreak severity; A), NDVI (prefire vegetation; B), elevation (C), FWI (fire weather; D), and RdNBR (burn severity; E).

CHAPTER 5: An added boost in pyrogenic carbon when wildland fires burn through forests with high pre-fire mortality[4]

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Keywords: Pyrogenic Carbon, Deep Char, scorch, biogeochemical cycles, biologic function, structural legacies, benzene polycarboxylic acid (BPCA) method, Oregon, Lodgepole pine

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[4] This chapter is formatted as a research note.

Abstract

The production of postfire pyrogenic carbon (PyC) depends on the state of a forest prior to wildfire. Substantial prefire tree mortality can alter the outcomes for postfire legacy structures that are more charred. The concentration of PyC on charred snags that develops during wildfire is poorly understood. We use the benzene polycarboxylic acid (BPCA) method to evaluate PyC on charred snags (i.e., dead prior to fire) and scorched snags (i.e., alive at time of fire). Charred snags had a greater concentration of PyC compared to scorched snags, which only had PyC on the bark. Fires that burn stands with substantial prefire mortality have the potential to leave a wood-based PyC legacy that can influence ecosystem function – carbon sequestration, water purification, and soil nutrient supply.

One Sentence Summary

Concentrations of pyrogenic carbon are greater on charred snags than scorched snags in forests with beetle outbreaks and wildfire.

Introduction

Wildland fire plays an important role mediating carbon pools in forest ecosystems globally. Pyrogenic carbon (PyC; referred to as soot, char, black carbon, scorch, charred biomass, deep char, and biochar) is the product of incomplete combustion of organic matter, and exists along a gradient of turnover rates that is dependent on its concentration and degree of aromatic condensation (i.e. direct linkage of benzene rings and sheets; Bird et al. 2015). Higher temperatures and extended periods of heating generally produce organic matter with higher concentrations of PyC and a greater degree of aromatic condensation (McBeath et al. 2011, Schneider et al. 2013, Bird et al. 2015); resulting in thermally altered organic matter that displays relatively longer turnover times as it interacts with its environment compared to other carbon pools (Masiello and Druffel 1998, Swift 2001, Torn et al. 2005). There is increasing recognition that charring is substantial when fires burn through forests with high levels of pre-fire tree mortality (i.e., abundant standing dead trees, or snags) from recent high-severity insect outbreaks (Harvey et al. 2014a; Talucci and Krawchuk 2019) or recent high severity wildfire (Donato et al. 2016; referred to as re-burn) in comparison to when fires burn through forests dominated by live trees. Here we use the term “charred snags” to refer to snags that subsequently burn generating deeply charred structural legacies in the forest and “scorched snags” to refer to trees that are killed by fire, resulting in a lighter scorched legacy from fire. Despite the current and predicted increases in short-interval disturbances such as insect outbreak followed by wildfire (Raffa et al. 2008, Flannigan et al. 2009, Bentz et al. 2010) that are likely to result in the widespread production of deeply charred snags on forested landscapes, the concentration of PyC associated with this charring is unknown. Most research has focused on the accumulation of PyC in soils due to fire (Santín et al. 2016). Understanding the molecular characteristics of this PyC pool is important for effective carbon budgeting, climate change modelling, and forest ecosystem science.

The concentration and aromatic condensation of PyC changes how it interacts with its environment, in turn influencing its turnover time (Bird et al. 2015). The PyC continuum includes a wide range of thermally altered material along a condensation gradient, ranging from slightly charred biomass that turns over relatively quickly to highly condensed aromatic material, such as soot, that may remain in the environment (e.g., soils and sediment) for centuries to millennia (Bird et al. 2015). Heating during pyrolysis can transform organic matter into benzene rings that fuse together to form condensed aromatic structures that can continue to extend into sheets, as demonstrated during heating in muffle furnace experiments (McBeath et al. 2011). The increase in condensation produces a higher proportion of rings with all six carbons bonded to other benzine rings, which has been positively correlated with resistance to microbial decay (Bird et al. 2015). There have been limited studies of PyC on snags/trees under wildfire conditions (Schneider et al. 2013), which are necessary for understanding PyC accumulation in the wild. An experimental forest fire showed a direct positive increase between the level of aromatic condensation and temperature for bark biomass on pitch pine (*Pinus rigida*), while needle and leaf biomass showed no or a negative relationship between heating temperature and aromatic condensation, respectively (Schneider et al. 2013). A fairly common and robust measure of PyC is a molecular marker method, benzene polycarboxylic acid (BPCA) analysis, that quantifies the amount of PyC in a sample (i.e., PyC/kg C or ‘PyC/kg material) (Dittmar 2008, Wiedemeier et al. 2016) and evaluates the degree of aromatic condensation with the Aromatic Condensation Index (ACI), which calculates the ratio of BPCAs from six carbon-carbon double bonds (B6CAs) to the total BPCA content.

Scorch and deep char are visually distinct characteristics in burned forests, and their production during wildfire is attributed to different mechanisms. Scorch on snags tends to cover the bark and is distinguished by a matte, black dusty appearance, while deep char on snags has the appearance of alligator scales and iridescent black coloring (Figure 5.1 and Figure 5.S3). The initial flaming front during a wildfire is the primary mechanism for scorch production on trees, while long smoldering burns produce deep char on snags that can continue burning after the initial flaming front has passed (Alexander 1982, Campbell et al. 2007). In comparison to live trees, snags are able to ignite faster (Stockstad 1979) and at lower temperatures (Stockstad 1975) due to reduced moisture content (Campbell et al. 2007). The prolonged burning time associated with smoldering and glowing combustion (Brown et al. 1985, Page and Jenkins 2007, Hyde et al. 2011) on snags can lead to torching – i.e., ignition and flare up (Wenger 1984), which can result in snags being encased by deep char. Often, the smoldering of large downed wood or standing snags extends well beyond when the initial flaming front moves through the area (Alexander 1982) facilitating the consumption of more biomass on snags than on trees alive at the time of fire (Brown et al. 2003, Hyde et al. 2011). Deep char is a prominent fire effect on snags that burn during wildfire and rarely occurs when live trees are killed by fire (Talucci and Krawchuk 2019, Donato et al. 2009, 2016, Harvey et al. 2014b). Current evaluation of deep char on snags is solely based on visual estimates of the proportional coverage on snags and/or downed wood (Tinker and Knight 2000, Donato et al. 2009, Santín et al. 2016, Ward et al. 2017). These visual estimates have yet to be linked to the quantitative concentration and condensation of PyC for the deep char that encases snags (Bird et al. 2015, Santín et al. 2016), yet could have wide ecological implications depending on its turnover time on the landscape.

We hypothesized that prolonged smoldering and glowing combustion that generates deep char on snags will involve pyrolysis that produces higher concentrations of PyC when compared to scorched snags. Accordingly, we proposed that aromatic condensation in samples from deeply charred snags would have larger concentrations of B6CAs compared to scorched snags. This hypothesis was anchored in the expectation that extended burning would result in more condensed PyC. To test our hypotheses, we used the BPCA method (Dittmar 2008, Wiedemeier et al. 2016) to measure the concentration and condensation of PyC for samples from charred and scorched snags collected in June 2018 from the Pole Creek fire that burned in 2012 on the eastside of the Cascade Mountains in the Deschutes National Forest, Oregon, U.S.A. Samples were acquired from an area where lodgepole pine (*Pinus contorta* var. *murrayana*) was dominant and experienced significant pre-fire mortality from mountain pine beetles (*Dendroctonus ponderosae*; Agne et al. 2016). We collected samples from three charred snags and three scorched snags. On charred snags, we collected charred material directly from exposed sections of wood and bark on the snag. For scorched snags, we collected scorched material directly exposed bark, and wood was sampled from underneath scorched material since no wood was directly exposed.

Results

Our results show that samples from charred snags contain higher concentrations of PyC than scorched snags. Charred snags had greater concentrations of PyC both as a proportion of carbon and as a proportion of total material compared to scorched snags (Figure 5.2A, B). On the charred snags, wood samples contained a higher concentration of PyC than bark samples for both per-carbon and per-material measurements (Figure 5.2A, B; table 5.S1-S2). On scorched snags, wood samples had a lower concentration of PyC than the bark samples for both per-carbon and per-material measurements (Figure 5.2A, B; table 5.S1-S2), as might be expected due to the high moisture content in live trees during wildfire, which limits ignition and extended heating (Stockstad 1975, 1979, Brown et al. 1985). The aromatic condensation index (ACI), which characterizes condensation levels, showed no evidence of a difference between charred snags and scorched snags (Figure 5.2; table 5.S3).

Discussion

Charred snags provide an added boost of PyC to forest ecosystems compared to scorched snags, revealing an important path of forest carbon dynamics in the context of wildfires interacting with previous forest disturbances. Charred snags are a legacy structure in which standing biomass is encased either partially or fully in PyC, which could influence ecosystem functions that operate through wood such as decomposition, carbon dynamics, nutrient cycling, and resources for insects and birds. We measured PyC in specific samples to ascertain the concentration and condensation of PyC, however further studies are needed to quantify the charring on snags to determine the amount of PyC at the stand or landscape scale. Our findings did not detect differences in condensation levels (as measured by ACI) between charred and scorched snags indicating that they experienced a similar thermal exposure during wildfire. This lack of thermal distinction was unexpected, since at time of fire scorched snags would have had a higher moisture content compared to charred snags and would be expected to produce more sheets increasing the aromatic condensation. Since heating would initially drive off moisture in live trees, we predicted this would limit thermal alterations of the scorched snag samples, but our findings did not offer this distinction. Temperature and duration of heating dictate the concentration and condensation of PyC on snags and potential longevity in the environment. Initially heating drives off water and volatile organic compounds, which is followed by the thermal alteration of organic matter and the development of PyC (Bird et al. 2015). We would not expect deep char in live trees due to the full bark coverage and high moisture levels, which would limit how the wood is thermally altered and subsequent PyC concentration and condensation of the wood under the bark. Forest conditions prior to wildfire are pivotal to shaping postfire form and function of wood-based ecological legacies. While our sample size is small and specific to a single fire that burned through a forest that had experienced mountain pine beetle outbreaks, the conditions are comparable to the extent of regional outbreaks that span western North American forests (Raffa et al. 2008). These characteristics can occur at scales of individual trees, stands of trees, and forested landscapes leading to considerations for broader conceptual effects related to ecosystem functions. Larger proportions of charred snags equate to a higher concentration of PyC across the landscape, which has the potential to influence processes that operate through wood legacies.

The legacies of dead wood are critical components of the ecosystem that serve various functions over time, and we need to know more about how the PyC signature on charred snags influences those functions reliant on dead wood (Figure 5.3). Decomposition, nutrient cycling, and microbial activity are all ecosystem processes that operate through the dead wood pool (Franklin et al. 1987, Harmon 2001). Short-interval disturbances (e.g., fire + fire, insect + fire, drought + fire) create unique conditions for dead wood by generating more PyC on legacy structures, and there is a need to understand the role of snags and logs encased in PyC on these ecosystem processes. The breakdown of charred snags through weathering and/or falling could mobilize PyC from snags to woody debris (Manies et al. 2005) to soil organic matter. Since charred snags have greater concentrations of PyC than scorched snags, they could contribute more PyC to soils over time and have the potential to slow turnover times for decomposition processes and subsequent carbon cycling (Bird et al. 2015) while scorched snags comparatively would result in relatively faster turnover rates. Whether PyC remains on standing snags or relocates from snags to the soil, the greater concentration of PyC on charred snags increases the amount of decay resistant carbon in the postfire landscape (Preston 2009, Bird et al. 2015), which may constrain microbial activity in wood (Bird et al. 2015). Constraints on microbial and fungal activity could alter the spatial and temporal decay processes by limiting decomposition and holding wood-based legacies at the surface longer, which could have cascading effects for nutrient cycling and soil carbon stabilization. However, charred wood-based legacies that persist could contribute to the fuel complex of the next fire (Doerr et al. 2018). The PyC legacy structures may influence ecosystem processes on spatial-temporal scales from individual trees to the landscape scale and from days to millennia.

Disturbances that recur over short intervals can reduce the abundance of wood-based legacy structures and increase the abundance of charred snags, which can influence postfire biodiversity (Figure 5.3). Short-interval fire + fire events (i.e., reburns) reduce the collection of dead wood (Donato et al. 2016, Ward et al. 2017) that contributes to structural and ecological legacies that serve as habitat, food sources, and nutrient cycling (Franklin et al. 2000, Swanson et al. 2011, Johnstone et al. 2016). Charred snags typically have a simplified structure, while trees killed by fire (scorched trees) tend to retain their canopy complexity (Talucci and Krawchuk 2019). A simplified snag structure could reduce perching habitat for birds, nesting material, shade cover, and the interception of precipitation. Charred snags fully encapsulated by PyC may reduce habitat for postfire specialists, particularly the resources needed by saproxylic insects and birds that rely on them. For example, in patches where over 50% of the trees are covered by char (96-100%), the abundance of saproxylic insects was reduced for conifer forests compared to areas that burned less severely in the eastern boreal region of Quebec, Canada (Nappi et al. 2010). Although this was not specifically linked to prolific pre-fire tree mortality, there is a logical link, and it begs the question of whether patches with a large proportion of charred snags alter the biodiversity of postfire specialists.

The abundance of charred snags from fire burning through landscapes with high existing levels of mortality from drought, insect outbreak, and previous wildfire events is becoming a more common legacy for contemporary western North American forests. Gradients of fire severity and tree mortality prior to wildfire yield a heterogeneous mosaic of patches across a landscape. Due to the variability across postfire burn mosaics, alterations in ecosystem functions associated with PyC concentrations could be subtle but might also be surprisingly pronounced; we know so little about this phenomenon. However, with predicted increases in the size, frequency, and intensity of broad-scale disturbances (Dale et al. 2001), the interactions between events (e.g., drought, insects, and wildfire) could compound the ecological response to fire, especially at the extreme ends where high severity burn patches could be larger and have greater concentrations of PyC. Increased research is needed to understand carbon implications of short-interval disturbances, and broader ecosystem implications– bringing together “silos” of fire + fire, insect + fire, and drought + fire to understand the ecological effects of burning through forests with substantial numbers of snags.

References and Notes

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

Alexander, M. E. 1982. Calculating and interpreting forest fire intensities. Canadian Journal of Botany 60:2185–2185.

Bentz, B. J., J. Regniere, C. J. Fettig, M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. Negron, and S. J. Seybold. 2010. Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects. BioScience 60:602–613.

Bird, M. I., J. G. Wynn, G. Saiz, C. M. Wurster, and A. McBeath. 2015. The Pyrogenic Carbon Cycle. Annual Review of Earth and Planetary Sciences 43:273–298.

Brown, J. K., M. A. Marsden, K. C. Ryan, and E. D. Reinhardt. 1985. Predicting Duff and Woody Fuel Consumed by Prescribed Fire in the Northern Rocky Mountains. Research Paper INT-337.

Brown, J. K., E. D. Reinhardt, and K. A. Kramer. 2003. Coarse woody debris: managing benefits and fire hazard in the recovering forest. USDA Forest Service Gen. Tech. Rep. 105:1–16.

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research: Biogeosciences 112:1–11.

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

Dittmar, T. 2008. The molecular level determination of black carbon in marine dissolved organic matter. Organic Geochemistry 39:396–407.

Doerr, S. H., C. Santín, A. Merino, C. M. Belcher, and G. Baxter. 2018. Fire as a Removal Mechanism of Pyrogenic Carbon From the Environment : Effects of Fire and Pyrogenic Carbon Characteristics 6:1–13.

Donato, D. C., J. L. Campbell, J. B. Fontaine, and B. E. Law. 2009. Quantifying char in postfire woody detritus inventories. Fire Ecology 5:104–115.

Donato, D. C., J. B. Fontaine, and J. L. Campbell. 2016. Burning the legacy? Influence of wildfire reburn on dead wood dynamics in a temperate conifer forest. Ecosphere 7:1–13.

Flannigan, M., B. Stocks, M. Turetsky, and M. Wotton. 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. Global Change Biology 15:549–560.

Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. Mckee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity: Ecosystem disturbances, biological legacies and ecosystem recovery. Conservation in Practice 1:8–17.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree Death as an Ecological Process: The causes, consequences, and variability of tree mortality. BioScience 37:550–556.

Harmon, M. E. 2001. Moving Towards a New Paradigm for Woody Detritus Management. Ecological Bulletins 49:269–278.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proceedings of the National Academy of Sciences 111:15120–15125.

Hyde, J. C., A. M. S. Smith, R. D. Ottmar, E. C. Alvarado, and P. Morgan. 2011. The combustion of sound and rotten coarse woody debris: A review. International Journal of Wildland Fire 20:163–174.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. W. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Manies, K. L., J. W. Harden, B. P. Bond-Lamberty, and K. P. O'Neill. 2005. Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage. Canadian Journal of Forest Research 35:472–482.

Masiello, C. A., and E. R. M. Druffel. 1998. Black carbon in deep-sea sediments. Science 280:1911–1913.

McBeath, A. V., R. J. Smernik, M. P. W. Schneider, M. W. I. Schmidt, and E. L. Plant. 2011. Determination of the aromaticity and the degree of aromatic condensation of a thermosequence of wood charcoal using NMR. Organic Geochemistry 42:1194–1202.

Nappi, A., P. Drapeau, M. Saint-Germain, and V. A. Angers. 2010. Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. International Journal of Wildland Fire 19:500–511.

Page, W. G., and M. J. Jenkins. 2007. Predicted fire behavior in selected mountain pine beetle infested lodgepole pine. Forest Science 53:662–674.

Preston, C. M. 2009. Fire's black legacy. Nature Geoscience 2:674–675.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. a. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. BioScience 58:501.

Santín, C., S. H. Doerr, E. S. Kane, C. A. Masiello, M. Ohlson, J. M. de la Rosa, C. M. Preston, and T. Dittmar. 2016. Towards a global assessment of pyrogenic carbon from vegetation fires. Global Change Biology 22:76–91.

Schneider, M. P. W., L. A. Pyle, K. L. Clark, W. C. Hockaday, C. A. Masiello, and M. W. I. Schmidt. 2013. Toward a "molecular thermometer" to estimate the charring temperature of wildland charcoals derived from different biomass sources. Environmental Science and Technology 47:11490–11495.

Stockstad, D. S. 1975. Spontaneous and piloted ignition of pine needles. Ogden, Utah.

Stockstad, D. S. 1979. Spontaneous and Piloted Ignition of Rotten Wood. Ogden, Utah.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.

Swift, R. S. 2001. Sequestration of carbon by soil. Soil Science 166:858–871.

Talucci, A. C., and M. A. Krawchuk. 2019. Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. Ecosphere 10(5):e02744. 10.1002/ecs2.2744

Tinker, D. B., and D. H. Knight. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3:472–483.

Torn, M. S., P. M. Vitousek, and S. E. Trumbore. 2005. The influence of nutrient availability on soil organic matter turnover estimated by incubations and radiocarbon modeling. Ecosystems 8:352–372.

Ward, A., C. A. Cansler, and A. J. Larson. 2017. Black Carbon on Coarse Woody Debris in Once- and Twice-Burned Mixed-Conifer Forest. Fire Ecology 13:143–147.

Wenger, K. F. 1984. Fire Management. Page 220 Forestry Handbook. John Wiley & Sons, New York.

Wiedemeier, D. B., S. Q. Lang, M. Gierga, S. Abiven, S. M. Bernasconi, G. L. Früh-Green, I. Hajdas, U. M. Hanke, M. D. Hilf, C. P. McIntyre, M. P. W. Scheider, R. H. Smittenberg, L. Wacker, G. L. B. Wiesenberg, and M. W. I. Schmidt. 2016. Characterization, Quantification and Compound-specific Isotopic Analysis of Pyrogenic Carbon Using Benzene Polycarboxylic Acids (BPCA). Journal of Visualized Experiments:1–9.

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Figures

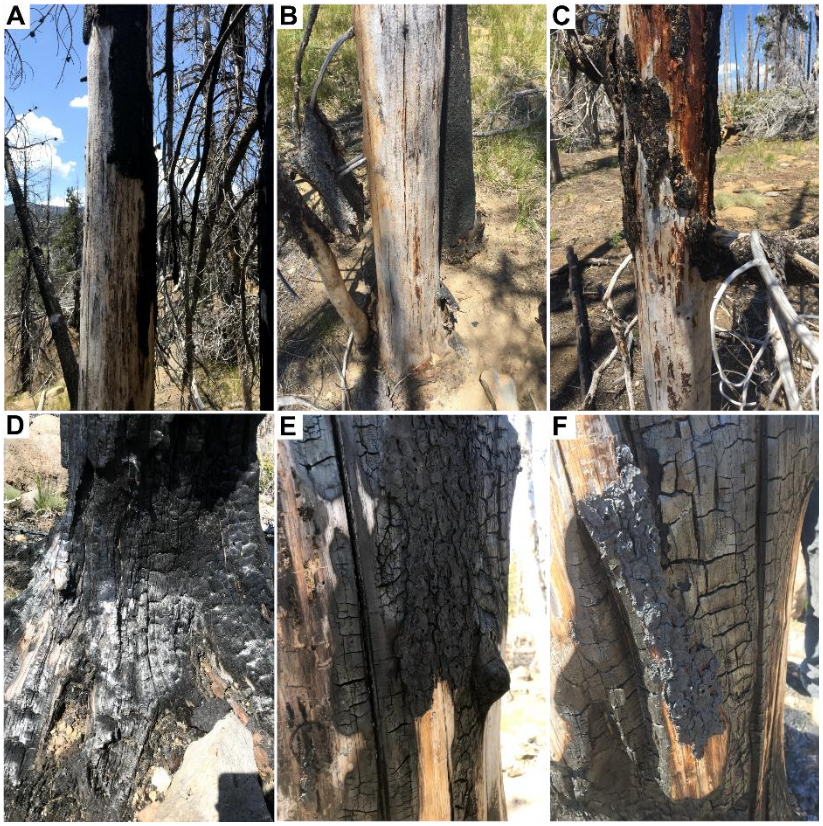

Figure 5.1. Examples of charred snags and scorched snags from the Pole Creek Fire. Panel **A-C** depicts trees that were live at time of fire, killed by fire, and had scorched bark. The underlying wood had no visual evidence of scorch or char and no evidence of mountain pine beetle activity. The bark has since started to slough off the snags and was on the ground surrounding the snags. Panel **D-F** show charred snags that had evidence of mountain pine beetle activity (i.e. J-shaped galleries), and were considered to be dead prior to the Pole Creek fire.

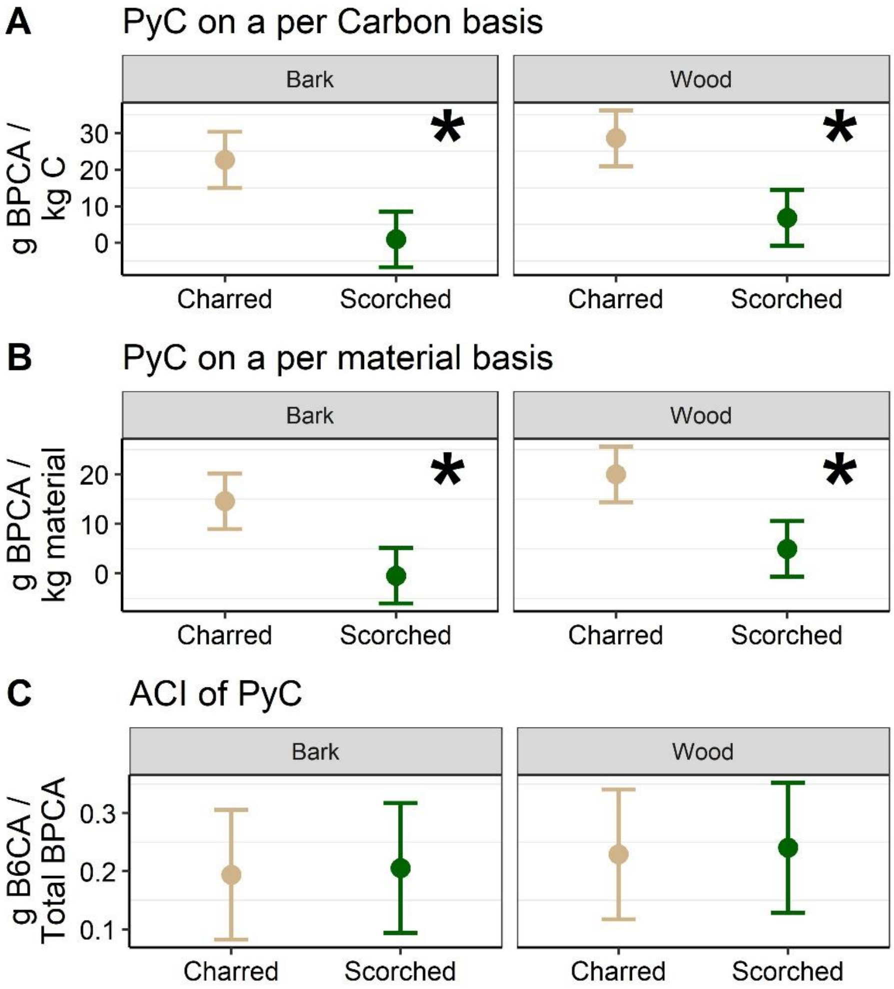

Figure 5.2. Difference in PyC on charred snags (i.e., charred) and scorched snags (i.e., scorched). PyC on a per-carbon (**A**) and per-material basis (**B**) is greatest on the wood of charred snags and this difference was statistically different (*). Both wood and bark on charred snags had higher concentrations of PyC compared to scorched snags. The Aromatic Condensation Index (ACI) indicates the proportion of B6CA concentrations to total BPCA with B6CA indicating six carbon-carbon double bonds (**C**). See Table 5.S1 for estimates, confidence intervals, and comparisons.

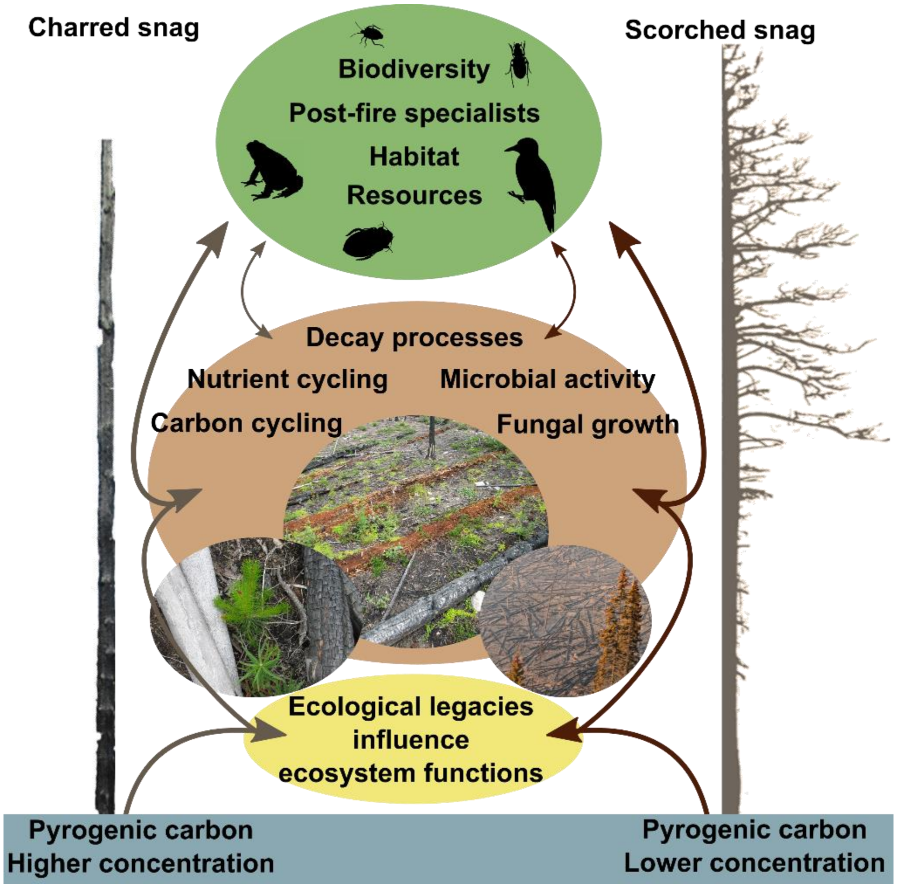

Figure 5.3. A conceptual framework of how postfire legacies, deep charring, and PyC influence ecosystem functions. The greater concentration of PyC on charred snags compared to scorched snags creates an ecological legacy that may function differently. Pictured here is a charred snag (left) with a greater concentration of PyC compared to the scorch snag (right). Under higher fire severity, the legacy of the charred snag is more simplistic compared to the scorched snag. Forest conditions that produce postfire legacies characterized by a substantial portion of charred snags could influence turnover time for processes that operate through wood-based legacies including decomposition, microbial and fungal activity, nutrient cycling, resources for insects and birds, as well as carbon cycling.

Methods

Sample collection

We collected samples from three charred snags and three scorched snags on June 19, 2018 from the area burned by the Pole Creek Fire in the Deschutes National Forest in the East Cascade Mountains of central Oregon. The benzene polycarboxylic acid (BPCA) method (described below) is a time-intensive organic geochemical procedure where small sample sizes are common and in-line with other research (e.g. Matosziuk et al. 2019). The Pole Creek Fire burned in 2012 through forests dominated by lodgepole pine (*Pinus contorta* var. *murrayana*) with significant prefire mortality from mountain pine beetles (*Dendroctonus ponderosae*; Agne et al. 2016). The samples came from "charred snags", which refer to snags that were killed by mountain pine beetles and subsequently burn generating deeply charred structural legacies in the forest, and from "scorched snags", which refer to trees that were killed by fire, resulting in a lighter scorched legacy from fire. We confirmed mountain pine beetle mortality by visible exit holes on bark and removing bark to identify j-shaped galleries in the cambium. We collected samples from three charred snags and three scorched snags. On charred snags, we collected charred material directly from exposed sections of wood and bark on the snag (Figure 5.S1). For scorched snags, we collected scorched material directly from exposed bark, and wood was sampled from underneath the most scorched section of bark since no wood was directly exposed during fire and was assumed to be the most thermally altered (Figure 5.S1).

Sample Preparation & Procedure

Samples were dried overnight at 50°C and ground using a ball mill (Klecko). Two of the bark samples, which came from scorched snags (i.e. trees killed by fire), contained sap residue, which made them tacky and difficult to homogenize. These two samples were dried at 50°C for an additional three days. Samples were then flash frozen in liquid nitrogen and ground into a fine powder with a mortar and pestle.

We used the benzene polycarboxylic acid (BPCA) method to quantify the PyC content and molecular structure of our samples. The BPCA method was developed by Glaser et al. (1998) and has since been refined (see Brodowski et al. 2005, Dittmar 2008, Wiedemeier et al. 2013, 2016). We adapted the methods developed by Dittmar (2008) and Wiedemeier et al. (2013, 2016). Briefly, samples containing 2 mg of organic carbon were digested in 5 mL nitric acid at 170°C for eight hours to break down the large aromatic structures that are characteristic of PyC into individual BPCAs. Samples were filtered through glass fiber filters (Whatman, GF/A), diluted to 50 mL with deionized water, flash frozen with liquid nitrogen and freeze dried (LabConco FreeZone Plus). The residue was brought up in 2 mL of 1M NaOH and filtered using 0.45 μm nylon syringe filters (Whatman). A 1 mL aliquot of this solution was transferred to a new vial and spiked with 600 μL of 2M HCl. High performance liquid chromatography (HPLC) was used to quantify individual BPCAs. Specifically, samples were analyzed using a Shimadzu LC-10AD equipped with an SPD-M20A photodiode array capable of measuring wavelengths between 190-400 nm. An Agilent Poroshell 120 SB-C18 column was used with a mobile phase consisting of a binary gradient of H_3PO_4 (2% in water) and acetonitrile (Wiedemeier et al. 2013). External standards of pure BPCA solutions (Sigma Aldrich) were used to construct 6-point calibration curves to determine the concentrations of individual BPCAs. We could support the low sample size due to the reproducibility of duplicate analyses outlined by Matoszuik et al. (2019), which includes further experimental details.

We assessed PyC on charred and scorch snags by measuring the concentration and degree of aromatic condensation. Concentration of PyC was measured as g BPCA per kg carbon and as g BPCA per kg material. The degree of aromatic condensation was quantified using the Aromatic Condensation Index (ACI), which is defined as the concentration of benezene hexacarboxylic acid (B6CA) as a proportion of all BPCAs. The data from our samples are shown in Figure 5.S2.

Statistical Analyses

We evaluated the difference in PyC concentrations and degree of aromatic condensation between charred and scorched snags for bark and wood samples. We assessed these differences with three response variables – BPCA per carbon weight, BPCA per material weight, and ACI. We conducted three analyses one for each response variable – PyC per carbon, PyC per material, and ACI. Each response variable was analyzed as a function of two factorial explanatory variables scorch or char and bark or wood. The sample size was small for each analysis (n=12) and particularly small when split across the factors of the explanatory variables – charred bark (n=3), scorched bark (n=3), charred wood (n=3), and scorched wood (n=3). We used generalized linear models with a Guassian distribution for continuous response variables. We used the "lsmeans" package for comparisons (Lenth 2016) to test for a difference in means between our charred and scorch snags for the bark and wood samples. We assessed assumptions for all models by visually inspecting the residuals, which appeared to be adequately met. We evaluated for overdispersion, which was not an issue. All statistical analyses were conducted in R statistical computing software version 3.4.4 (R Development Team 2018). We considered $p < 0.05$ as convincing evidence of a relationship and $p < 0.10$ as suggestive of a relationship to minimize the potential of a Type II error. Data and code for analyses are available online (Talucci 2019).

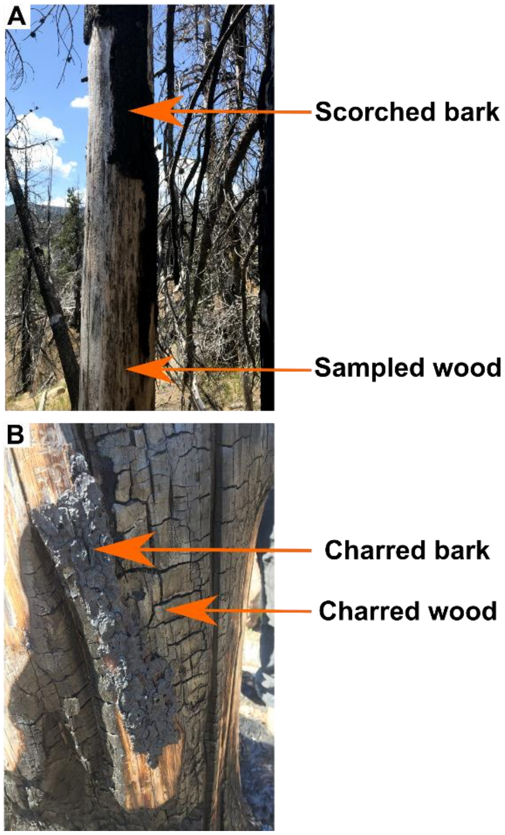

Figure 5.S1. Examples of charred and scorched samples. Panel **A** shows a sampled snag that was killed by fire with no evidence of mountain pine beetle activity. Samples were taken from the scorched bark and from the wood under scorched bark. Panel **B** shows a snag that was killed prior to the fire with evidence of mountain pine beetle activity. Samples were taken from the charred bark and charred wood.

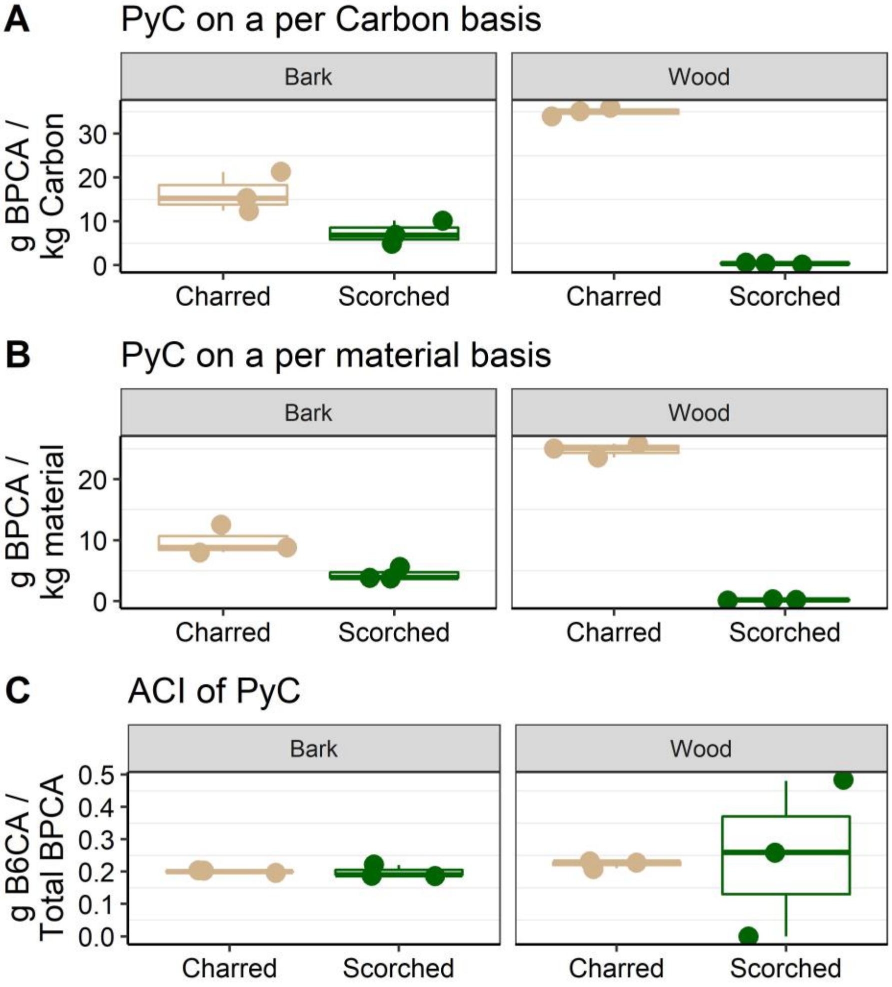

Figure 5.S2. Raw data samples. The distribution of the raw data samples for the concentration of PyC for charred and scorched snags on a per kg carbon (**A**) and per kg material basis (**B**) for both bark and wood samples. The degree of aromatic condensation, ACI of PyC is similar across all samples (**C**). The ACI values for scorched wood are variable due to the very low levels of BPCA.

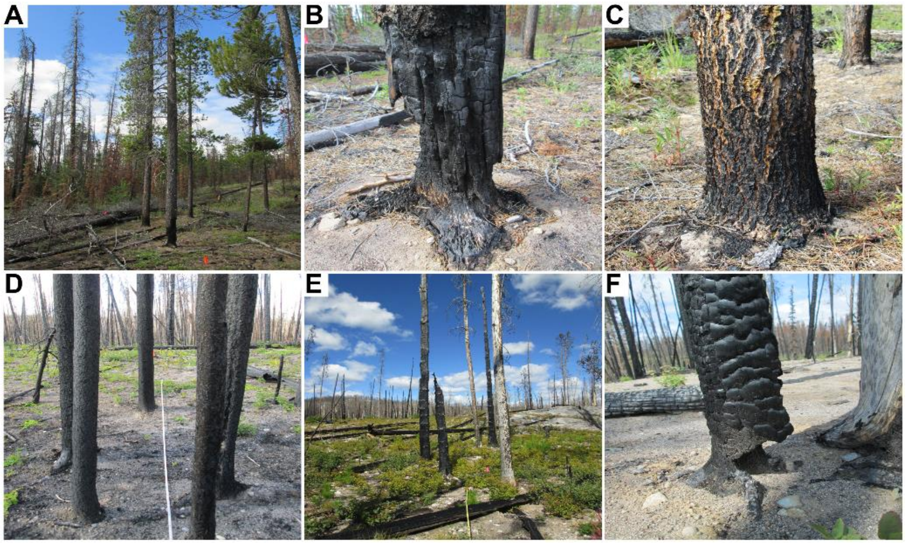

Figure 5.S3. Additional examples of charred and scorched snags. Panel **A** depicts two adjacent trees, one snag with deep char at the base (**B**) and one live tree with scorch at the base (**C**). In panel **D**, scorched bark is depicted on trees that were killed by wildfire. Panel **E** demonstrates a collection of deep charred snags (left) adjacent to trees that were scorched and shed their bark (right). In Panel **F**, deep char is evident on the stem to the left, while the stem to the right experiened scorch shed its bark. Photos are from fires that burned through lodgepole pine forest in central interior British Columbia, Canada.

Table 5.S1. Analysis estimates and confidence intervals for BPCA analysis. BPCA per Carbon (g BPCA / kg Carbon) corresponds to Figure 5.1 panel A. BPCA per material (g BPCA / kg material) corresponds to Figure 5.1 panel B. ACI (g B6CA / Total BPCA) corresponds to Figure 5.1 panel C.

Sample	Estimate	95% CI		p-value	Comparison
		Lower	Upper		
BPCA per Carbon (g BPCA / kg Carbon)					
Charred snag -wood	28.59	20.95	36.23	**<0.0001**	a
Scorched snag - wood	6.81	-0.83	14.45	**<0.0001**	b
Charred snag - bark	22.7	15.07	30.35	**<0.0001**	a
Scorched snag -bark	0.93	-6.71	8.57	1	b
BPCA per material (g BPCA / kg material)					
Charred snag -wood	20.01	14.41	25.62	**<0.0001**	c
Scorched snag - wood	5.00	-0.60	10.61	1	d
Charred snag - bark	14.61	9.00	20.21	**<0.0001**	c
Scorched snag -bark	-0.40	-6.00	5.21	0.160	d
ACI (g B6CA / Total BPCA)					
Charred snag -wood	0.22	0.11	0.34	**<0.0001**	e
Scorched snag - wood	0.24	0.12	0.35	**<0.0001**	e
Charred snag - bark	0.19	0.08	0.31	**0.0013**	e
Scorched snag -bark	0.20	0.09	0.32	**<0.0001**	e

References and Notes

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

Brodowski, S., A. Rodionov, L. Haumaier, B. Glaser, and W. Amelung. 2005. Revised black carbon assessment using benzene polycarboxylic acids. Organic Geochemistry 36:1299–1310.

Dittmar, T. 2008. The molecular level determination of black carbon in marine dissolved organic matter. Organic Geochemistry 39:396–407.

Glaser, B., L. Haumaier, G. Guggenberger, and W. Zech. 1998. Black carbon in soils: The use of benzenecarboxylic acids as specific markers. Organic Geochemistry 29:811–819.

Lenth, R. V. 2016. Least-Squares means: the R package lsmeans. Journal of Statistical Software 69:1–33.

Matosziuk, L. 2018. Effects of Season and Interval of Prescribed Burns on Pyrogenic Carbon Cycling in Ponderosa Pine Stands in Malheur National Forest. Oregon State University.

Matosziuk, L. M., Y. Alleau, B. K. Kerns, J. Bailey, and M. G. Johnson. 2019. Supporting Information Effects of season and interval of prescribed burns on pyrogenic carbon in ponderosa pine stands in Malheur National Forest. Geoderma:1–12.

R Development Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Talucci, A. C. (2019). Data and code: Pyrogenic Carbon (Version v0.1) [Data set]. Zenodo. http://doi.org/10.5281/zenodo.3235815

Wiedemeier, D. B., M. D. Hilf, R. H. Smittenberg, S. G. Haberle, M. W. I. Schmidt, W. D.B., H. M.D., S. R.H., H. S.G., and S. M.W.I. 2013. Improved assessment of pyrogenic carbon quantity and quality in environmental samples by high-performance liquid chromatography. Journal of Chromatography A 1304:246–250.

Wiedemeier, D. B., S. Q. Lang, M. Gierga, S. Abiven, S. M. Bernasconi, G. L. Früh-Green, I. Hajdas, U. M. Hanke, M. D. Hilf, C. P. McIntyre, M. P. W. Scheider, R. H. Smittenberg, L. Wacker, G. L. B. Wiesenberg, and M. W. I. Schmidt. 2016. Characterization, Quantification and Compound-specific Isotopic Analysis of Pyrogenic Carbon Using Benzene Polycarboxylic Acids (BPCA). Journal of Visualized Experiments:1–9.

CHAPTER 6: CONCLUSIONS

This research provides insight into interacting disturbances as a component of forest ecosystem dynamics for broad-scale MPB outbreaks and wildfires across sub-boreal forests in British Columbia. Due to the extent of tree mortality across British Columbia, legacy structures from the outbreaks will persist for decades influencing wildfire and wildfire legacies across these landscapes that are characterized by mixtures of live and dead trees. Understanding the nuances of interacting disturbances, particularly when substantial tree mortality events are followed by wildfire, is important for forest ecosystem science. Increasingly, wildfires will be burning through forests with substantial mortality from drought, insect outbreaks, and recent fire activity referred to as re-burns. Recognizing the outcomes that can ensue from these disturbance interactions including altered legacy structures, pyrogenic carbon, and ecosystem response will be critical to understanding the future of forest ecosystems. In summary, the key findings from this dissertation include:

1. **In sub-boreal forests with substantial tree mortality, dead snags burn differently than live trees.** Prefire snags from MPB outbreaks burn differently than trees that are alive at time of fire. Results from Chapters 2 and 5 show that snags have a greater probability of generating deep char (chapter 2) and that deep char on snags has a greater concentration of pyrogenic carbon (chapter 5). Both confirm that snags experience prolonged, smoldering burns, while live trees have enough moisture to limit ignition and combustion (Stockstad 1975, 1979, Campbell et al. 2007, Hyde et al. 2011). Fire severity – as represented by typical fire effects – was not influenced by outbreak severity, and instead can be attributed to burning conditions and fire weather (Chapter 2).

2. **Fire severity alters the postfire legacy structure for sub-boreal forest with pervasive mortality from MPB outbreaks.** Outbreak severity influences fire severity in terms of the legacy structure that persists after fire. Results from chapters 2, 3, and 5 demonstrate that the legacy structure that persists when snags burn can be more simplistic and covered with more deep char than when live trees burn (Chapter 2 and 3). I was able to link deep char to pyrogenic carbon concentrations that differ in comparison to those from scorched snags, altering the chemical-carbon legacy structure that persists (Chapter 5).
3. **In sub-boreal forest, gradients in fire severity contribute to heterogeneity in stand initiation of lodgepole pine recruitment.** Fire severity is a key mechanism that facilitates seed release from serotinous cones. Across gradients of fire severity (Chapter 2 and 3) – crown, severe surface, light surface, and unburned fire refugia – lodgepole pine seedling recruitment varied from high-density even-aged cohorts to low-density even-aged or mixed-aged cohorts (Chapter 3). Cone abundance was an important driver of recruitment and despite potential loss of the seedbank due to stand break down from outbreaks, a substantial seed source remains in these gray phase outbreak-affected forests to facilitate regeneration (Chapter 3).
4. **Landscape-scale assessments indicated that fuels, and MPB outbreak contributions to fuels, are important drivers of high burn severity.** Fuels are an important contributor of high burn severity especially when they are a mixture of live and dead fuels (Chapter 4). This link between fuels and severity is supported by both our landscape assessment (Chapter 4) and field-based evaluations that indicated increased woody biomass consumption on snags (Chapter 2). These findings indicate that the mixture of live and dead fuels on landscapes with the legacy of MPB are an important driver of

remotely sensed burn severity in conjunction with dry and windy climate conditions necessary for sub-boreal forests to burn.

5. **Sub-boreal forests are generally resilient after MPB outbreaks and wildfire.** Recruitment density of young lodgepole pine showed that these forests are generally resilient to multiple disturbances in close succession even with large portions of the landscape experiencing high burn severity (Chapter 4) and with more woody-biomass consumption during wildfire (Chapter 2). Previous research had indicated reductions in seedbanks associated with stand breakdown from MPB outbreaks (Teste et al. 2011), but recruitment densities generally exceeded pre-disturbance stand density in my studies, indicating that seedbanks are generally robust enough a decade after MPB attack to support postfire regeneration (Chapter 3). Although the fate of these early recruits through the stem exclusion phase and in concert with long-term postfire growing conditions still needs to be determined, I did observe some areas that burned at high severity with limited seedling establishment, indicating that some areas may be slow to regenerate or could serve as possible niches for slow shifts in species composition in response to global change (Johnstone et al. 2016, Stralberg et al. 2018).

Literature Cited

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research: Biogeosciences 112:1–11.

Hyde, J. C., A. M. S. Smith, R. D. Ottmar, E. C. Alvarado, and P. Morgan. 2011. The combustion of sound and rotten coarse woody debris: A review. International Journal of Wildland Fire 20:163–174.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. W. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Stockstad, D. S. 1975. Spontaneous and piloted ignition of pine needles. Ogden, Utah.

Stockstad, D. S. 1979. Spontaneous and Piloted Ignition of Rotten Wood. Ogden, Utah.

Stralberg, D., X. Wang, M.-A. Parisien, F.-N. Robinne, P. Sólymos, C. L. Mahon, S. E. Nielsen, and E. M. Bayne. 2018. Wildfire-mediated vegetation change in boreal forests of Alberta, Canada. Ecosphere 9:e02156.

Teste, F. P., V. J. Lieffers, and S. M. Landhäusser. 2011. Seed Release in Serotinous Lodgepole Pine Forests After Mountain Pine Beetle Outbreak. Ecological Applications 21:150–162.

BIBLIOGRAPHY

Abatzoglou, J. T., S. Z. Dobrowski, S. A. Parks, and K. C. Hegewisch. 2018. Terraclimate, a high-resolution global dataset of monthly climate and climate water balance from 1958-2015. Scientific Data.

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

Alexander, M. E. 1982. Calculating and interpreting forest fire intensities. Canadian Journal of Botany 60:2185–2185.

Alexander, M. E., and W. J. De Groot. 1988. Fire Behavior in Jack Pine Stands as related to the Canadian Forest Fire Weather Index (FWI) System. Canadian Forestry Service, Northwest Region, Edmonton, Alberta, Canada.

Alexander, M. E., and M. G. Cruz. 2012. Interdependencies between flame length and fireline intensity in predicting crown fire initiation and crown scorch height. International Journal of Wildland Fire 21:95–113.

Alexander, M. E., and M. G. Cruz. 2012. Modelling the impacts of surface and crown fire behavior on serotinous cone opening in jack pine and lodgepole pine forests. International Journal of Wildland Fire 21:709–721.

Astrup, R., K. D. Coates, and E. Hall. 2008. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. Forest Ecology and Management 256:1743–1750.

Axelson, J. N., R. I. Alfaro, and B. C. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. Forest Ecology and Management 257:1874–1882.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Batllori, E., J. J. Camarero, J. M. Ninot, and E. Gutiérrez. 2009. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. Implications and potential responses to climate warming. Global Ecology and Biogeography 18:460–472.

BCMFLNRO. 2012. Vegetation Resources Inventory. British Columbia Ministry of Forests Lands and Natural Resource Operations, Victoria, BC, Canada.

BCMFLNRO. 2016. Aerial Overview Survey Data Files. https://www2.gov.bc.ca/gov/content/environment/research-monitoring-reporting/monitoring/aerial-overview-surveys/data-files.

BCWS. 2016. Historical fire perimeters. British Columbia Wildfire Service, Victoria, BC.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Notes and observations: Aspect transformation in site productivity research. Journal of Forestry 64:691–692.

Bentz, B. J., J. Regniere, C. J. Fettig, M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. Negron, and S. J. Seybold. 2010. Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects. BioScience 60:602–613.

Bessie, W. C., and E. A. Johnson. 1995. The Relative Importance of Fuels and Weather on Fire Behavior in Subalpine Forests. Ecology 76:747–762.

Bird, M. I., J. G. Wynn, G. Saiz, C. M. Wurster, and A. McBeath. 2015. The Pyrogenic Carbon Cycle. Annual Review of Earth and Planetary Sciences 43:273–298.

Brown, J. K., M. A. Marsden, K. C. Ryan, and E. D. Reinhardt. 1985. Predicting Duff and

Woody Fuel Consumed by Prescribed Fire in the Northern Rocky Mountains. Research Paper INT-337.

Brown, J. K., E. D. Reinhardt, and K. A. Kramer. 2003. Coarse woody debris: managing benefits and fire hazard in the recovering forest. USDA Forest Service Gen. Tech. Rep. 105:1–16.

Brodowski, S., A. Rodionov, L. Haumaier, B. Glaser, and W. Amelung. 2005. Revised black carbon assessment using benzene polycarboxylic acids. Organic Geochemistry 36:1299–1310.

Brodrick, P. G., G. P. Asner, and P. G. Brodrick. 2017. Remotely Sensed Predictors of Conifer Tree Mortality During Severe Drought. Environmental Research Letters 12:1–9.

Buma, B., and C. A. Wessman. 2011. Disturbance interactions can impact resilience mechanisms of forests. Ecosphere 2:1–13.

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research: Biogeosciences 112:1–11.

Carlson, M. 2008. East-west trend of decreasing serotiny, relayed through mountain pine beetle seedling planning.

Cartwright, J. 2018. Landscape topoedaphic features create refugia from drought and insect disturbance in a lodgepole and whitebark pine forest. Forests 9:715.

Cichowski, D., and D. Morgan. 2009. Tweedsmuir-Entiako Caribou Population: Summary of Ecology and Effects of Disturbance. Smithers, BC.

Clark, J. A., R. A. Loehman, and R. E. Keane. 2017. Climate changes and wildfire alter vegetation of Yellowstone National Park, but forest cover persists. Ecosphere 8.

Coops, N. C., T. Hermosilla, M. A. Wulder, J. C. White, and D. K. Bolton. 2018. A thirty year, fine-scale, characterization of area burned in Canadian forests shows evidence of regionally increasing trends in the last decade. PLoS ONE 13:1–19.

Countryman, C. M. 1972. The fire environment concept. Berkeley, CA.

Crossley, D. I. 1956. Effect of crown cover and slash density on the release of seed from slash-borne lodgepole pine cones. Page Forest Research Divsion Technical Note No. 41. Canada.

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

De’ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192.

Delong, S. C. 1998. Natural disturbance rate and patch size distribution of forests in northern British Columbia : implications for forest management 72.

DeLong, S. C., and W. B. Kessler. 2000. Ecological characteristics of mature forest remnants by wildfire. Forest Ecology and Management 131:93–106.

Dillon, G. K., Z. A. Holden, P. Morgan, M. A. Crimmins, E. K. Heyerdahl, and C. H. Luce. 2011. Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. Ecosphere 2:1–33.

Dittmar, T. 2008. The molecular level determination of black carbon in marine dissolved organic matter. Organic Geochemistry 39:396–407.

Doerr, S. H., C. Santín, A. Merino, C. M. Belcher, and G. Baxter. 2018. Fire as a Removal Mechanism of Pyrogenic Carbon From the Environment : Effects of Fire and Pyrogenic Carbon Characteristics 6:1–13.

Donato, D. C., J. L. Campbell, J. B. Fontaine, and B. E. Law. 2009. Quantifying char in postfire woody detritus inventories. Fire Ecology 5:104–115.

Donato, D. C., J. B. Fontaine, and J. L. Campbell. 2016. Burning the legacy? Influence of wildfire reburn on dead wood dynamics in a temperate conifer forest. Ecosphere 7:1–13.

Edwards, M., M. A. Krawchuk, and P. J. Burton. 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire. Forest Ecology and Management 338:163–175.

Eidenshink, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, S. Howard, S. Falls, and S. Falls. 2007. A Project for Monitoring Trends in Burn Severity. Fire Ecology 3:3–21.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. The Journal of animal ecology 77:802–13.

Finney, M., I. C. Grenfell, and C. W. McHugh. 2009. Modeling containment of large wildfires using generalized linear mixed-model analysis. Forest Science 55:249–255.

Flannigan, M., B. Stocks, M. Turetsky, and M. Wotton. 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. Global Change Biology 15:549–560.

Fontaine, J. B., D. C. Donato, W. D. Robinson, B. E. Law, and J. B. Kauffman. 2009. Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. Forest Ecology and Management 257:1496–1504.

Francis, S. R., S. Skinner, M. Gallagher, and C. Marion. 2002. Characterising fire regimes: Fire history research in the SBPS and SBS biogeoclimatic zones of the Cariboo Forest Region. Williams Lake, British Columbia, British Columbia.

Franklin, J. F., D. Lindenmayer, J. A. MacMahon, A. Mckee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity: Ecosystem disturbances, biological legacies and ecosystem recovery. Conservation in Practice 1:8–17.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree Death as an Ecological Process: The causes, consequences, and variability of tree mortality. BioScience 37:550–556.

Friedman, J. 2001. Greedy Function Approximation : A Gradient Boosting Machine. The Annals of Statistics 29:1189–1232.

GeoBC. 2012. 2012 Digital Air Photos of B.C. GeoBC, Vancover, BC.

Glaser, B., L. Haumaier, G. Guggenberger, and W. Zech. 1998. Black carbon in soils: The use of benzenecarboxylic acids as specific markers. Organic Geochemistry 29:811–819.

Gonzalez, P., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Global Ecology and Biogeography 19:755–768.

Goodwin, N. R., N. C. Coops, M. A. Wulder, S. Gillanders, T. A. Schroeder, and T. Nelson. 2008. Estimation of insect infestation dynamics using a temporal sequence of Landsat data. Remote Sensing of Environment 112:3680–3689.

Hamann, A., and T. Wang. 2018. Climate BC/WNA/NA. http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/#ClimateBC.

Hansen, W. D., K. H. Braziunas, W. Rammer, R. Seidl, and M. G. Turner. 2018. It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99:966–977.

Harmon, M. E. 2001. Moving Towards a New Paradigm for Woody Detritus Management. Ecological Bulletins 49:269–278.

Hart, S. J., T. Schoennagel, T. T. Veblen, and T. B. Chapman. 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proceedings of the National Academy of Sciences of the United States of America 112:4375–80.

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

Harvey, B. J., R. A. Andrus, and S. C. Anderson. 2019. Incorporating biophysical gradients and uncertainty into burn severity maps in a temperate fire-prone forested region. Ecosphere 10:1–20.

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecological Applications 24:1608–1625.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2014. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proceedings of the National Academy of Sciences 111:15120–15125.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984-2010). Landscape Ecology 31:2367–2383.

Hermosilla, T., M. A. Wulder, J. C. White, N. C. Coops, and G. W. Hobart. 2015. An integrated Landsat time series protocol for change detection and generation of annual gap-free surface reflectance composites. Remote Sensing of Environment 158:220–234.

Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2016. dismo: species distribution modeling. R Package version 1.0-1.15.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367–368.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Hopkins, A. D. 1909. Practical information on the Scolytid beetles of North American forests. Page Barkbeetles of the genus Dendroctonous. Washington, DC.

House, K. N. 2014. Bird and beetle assemblages in mountain pine beetle killed forests and those subsequently burned: evidence for an effect of compound natural disturbances in British Columbia. Simon Fraser University.

Hunt, E. R., B. N. Rock, and P. S. Nobel. 1987. Measurement of leaf relative water content by infrared reflectance. Remote Sensing of Environment 22:429–435.

Hyde, J. C., A. M. S. Smith, R. D. Ottmar, E. C. Alvarado, and P. Morgan. 2011. The combustion of sound and rotten coarse woody debris: A review. International Journal of Wildland Fire 20:163–174.

Inouye, D. W. 2000. The ecological and evolutionary significance of frost in the context of climate change. Ecology Letters 3:457–463.

Jenkins, M. J., W. G. Page, E. G. Hebertson, and M. E. Alexander. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in Western North America and implications for fire management. Forest Ecology and Management 275:23–34.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. W. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Kennedy, R. E., Z. Yang, and W. B. Cohen. 2010. Remote Sensing of Environment Detecting trends in forest disturbance and recovery using yearly Landsat time series : 1 . LandTrendr — Temporal segmentation algorithms. Remote Sensing of Environment 114:2897–2910.

Kennedy, R. E., Z. Yang, W. B. Cohen, E. Pfaff, J. Braaten, and P. Nelson. 2012. Spatial and temporal patterns of forest disturbance and regrowth within the area of the Northwest Forest Plan. Remote Sensing of Environment 122:117–133.

Kennedy, R. E., Z. Yang, N. Gorelick, J. Braaten, L. Cavalcante, W. Cohen, and S. Healey. 2018. Implementation of the LandTrendr Algorithm on Google Earth Engine. Remote Sensing 10:691.

Key, C. H., and N. C. Benson. 2006. Landscape assessment (LA): Sampling and analysis methods. USDA Forest Service General Technical Report RMS-GTR-164-CD:1–55.

Kincaid, T. M., and A. R. Olsen. 2017. spsurvey: Spatial Survey Design and Analysis. R Packages version 3.4.

Klutsch, J. G., M. A. Battaglia, D. R. West, S. L. Costello, and J. F. Negron. 2011. Evaluating Potential Fire Behavior in Lodgepole Pine-Dominated Forests after a Mountain Pine Beetle Epidemic in North-Central Colorado. Western Journal of Applied Forestry 26:101–109.

Kolden, C. A., J. A. Lutz, C. H. Key, J. T. Kane, and J. W. Van Wagtendonk. 2012. Mapped versus actual burned area within wildfire perimeters : Characterizing the unburned. Forest Ecology and Management:38–47.

Krawchuk, A. M. A., S. G. Cumming, M. D. Flannigan, and R. W. Wein. 2006. Biotic and Abiotic Regulation of Lightning Fire Initiation in the Mixedwood Boreal Forest. Ecology 87:458–468.

Krawchuk, M. A., S. L. Haire, J. Coop, M. A. Parisien, E. Whitman, G. Chong, and C. Miller. 2016. Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. Ecosphere 7.

Krawchuk, M. A., and M. A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. Ecology 92:121–132.

Kulakowski, D., and T. T. Veblen. 2007. Effect of Prior Disturbances on the Extent and Severity of Wildfire in Colorado Subalpine Forests. Ecology 88:759–769.

Lamont, B. B., D. C. Le Maitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. Botanical Review 57:277–317.

Lenth, R. V. 2016. Least-Squares means: the R package lsmeans. Journal of Statistical Software 69:1–33.

Lewis, K. J., and I. D. Hartley. 2005. Rate of deterioration, degrade and fall of trees killed by mountain pine beetle: a synthesis of the literature and experiential knowledge. Page Mountain Pine Beetle Initiative.

Lotan, J. E. 1976. Cone serotiny - fire relationships in lodgepole pine. Tall Timbers Fire Ecology Conference Proceedings 14:267–278.

Lotan, J. E., J. K. Brown, and L. F. Neuenschwander. 1985. Role of fire in lodgepole pine forests. Pages 133–152 *in* D. Baumgartner, editor. Lodgepole pine the species and its management. Lodgepole pine the species and its management Symposium Proceedings, Washington State University, Pullman.

Lotan, J. E., and D. A. Perry. 1983. Ecology and regeneration of lodgepole pine. U.S. Department of Agriculture, Forest Service, Washington, DC.

Macias Fauria, M., and E. A. Johnson. 2008. Climate and wildfires in the North American boreal forest. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2317–2329.

Manies, K. L., J. W. Harden, B. P. Bond-Lamberty, and K. P. O'Neill. 2005. Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage. Canadian Journal of Forest Research 35:472–482.

Masiello, C. A., and E. R. M. Druffel. 1998. Black carbon in deep-sea sediments. Science 280:1911–1913.

Matosziuk, L. 2018. Effects of Season and Interval of Prescribed Burns on Pyrogenic Carbon Cycling in Ponderosa Pine Stands in Malheur National Forest. Oregon State University.

Matosziuk, L. M., Y. Alleau, B. K. Kerns, J. Bailey, and M. G. Johnson. 2019. Supporting Information Effects of season and interval of prescribed burns on pyrogenic carbon in ponderosa pine stands in Malheur National Forest. Geoderma:1–12.

McBeath, A. V., R. J. Smernik, M. P. W. Schneider, M. W. I. Schmidt, and E. L. Plant. 2011. Determination of the aromaticity and the degree of aromatic condensation of a thermosequence of wood charcoal using NMR. Organic Geochemistry 42:1194–1202.

McCarley, T. R., C. A. Kolden, N. M. Vaillant, A. T. Hudak, A. M. S. Smith, B. M. Wing, B. S. Kellogg, and J. Kreitler. 2017. Multi-temporal LiDAR and Landsat quantification of fire-induced changes to forest structure. Remote Sensing of Environment 191:419–432.

Meddens, A. J. H., C. A. Kolden, J. A. Lutz, A. M. S. Smith, C. A. Cansler, J. T. Abatzoglou, G. W. Meigs, W. M. Downing, and M. A. Krawchuk. 2018. Fire refugia: what are they, and why do they matter for global change? BioScience.

Meigs, G. W., J. L. Campbell, H. S. J. Zald, J. D. Bailey, D. C. Shaw, and R. E. Kennedy. 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? 6:118.

Meigs, G. W., R. E. Kennedy, and W. B. Cohen. 2011. A Landsat time series approach to characterize bark beetle and defoliator impacts on tree mortality and surface fuels in conifer forests. Remote Sensing of Environment 115:3707–3718.

Meigs, G. W., H. S. J. Zald, J. L. Campbell, W. S. Keeton, and R. E. Kennedy. 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environmental Research Letters 11.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.

Muir, P. S., and J. E. Lotan. 1985. Serotiny and life history of Pinus contorta var. latifolia. Canadian Journal of Botany 63:938–945.

Nappi, A., P. Drapeau, M. Saint-Germain, and V. A. Angers. 2010. Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. International Journal of Wildland Fire 19:500–511.

Nash, C. H., and E. A. Johnson. 1996. Synoptic climatology of lightning-caused forest fires in subalpine and boreal forests. Canadian Journal of Forest Research 26:1859–1874.

Page, W. G., and M. J. Jenkins. 2007. Predicted fire behavior in selected mountain pine beetle infested lodgepole pine. Forest Science 53:662–674.

Paine, R. T., M. J. Tegner, and E. a. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1:535–545.

Parisien, M.-A., and M. A. Moritz. 2009. Environmental controls on the distribution of wildfire at multiple spatial scales. Ecological Monographs 79:127–154.

Parks, S. A. 2014. Mapping day-of-burning with coarse-resolution satellite fire-detection data. International Journal of Wildland Fire 23:215.

Parks, S. A., L. M. Holsinger, M. H. Panunto, W. M. Jolly, S. Z. Dobrowski, and G. K. Dillon. 2018. High-severity fire: Evaluating its key drivers and mapping its probability across western US forests. Environmental Research Letters 13.

Parminter, J. 1992. Typical historic patterns of wildfire disturbance by biogeoclimatic zone. Minsitry of Forests, Victoria, British Columbia, Canada.

Perrakis, D. D. B., R. a. Lanoville, S. W. Taylor, and D. Hicks. 2014. Modeling Wildfire Spread in Mountain Pine Beetle-Affected Forest Stands, British Columbia, Canada. Fire Ecology 10:10–35.

Petrie, M. D., A. M. Wildeman, J. B. Bradford, R. M. Hubbard, and W. K. Lauenroth. 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. Forest Ecology and Management 361:328–338.

Preston, C. M. 2009. Fire's black legacy. Nature Geoscience 2:674–675.

Potter, B. E. 2012. Atmospheric interactions with wildland fire behaviour - II. Plume and vortex dynamics. International Journal of Wildland Fire 21:802.

R Development Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. a. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. BioScience 58:501.

Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985-2010). Ecosphere 8:e01695.

Reinhardt, E. D., R. E. Keane, and J. K. Brown. 2001. Modeling fire effects. International Journal of Wildland Fire 10:373–380.

Renard, S. M., E. J. B. Mcintire, and A. Fajardo. 2016. Winter conditions - not summer temperature - influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec. Journal of Vegetation Science 27:29–39.

Ridgeway, G. 2015. gbm: generalized boosted regression models. R package version 1.3-5.

Robinson, N. M., S. W. J. Leonard, E. G. Ritchie, M. Bassett, E. K. Chia, S. Buckingham, H. Gibb, A. F. Bennett, and M. F. Clarke. 2013. Refuges for fauna in fire-prone landscapes: Their ecological function and importance. Journal of Applied Ecology 50:1321–1329.

Roy, D. P., V. Kovalskyy, H. K. Zhang, E. F. Vermote, L. Yan, S. S. Kumar, and A. Egorov. 2016. Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. Remote Sensing of Environment 185:57–70.

Ryan, K., and W. J. Elliot. 2005. Fire effects and soil erosion models. Pages 171–177 *in* D. G.

Neary, K. C. Ryan, and L. F. DeBano, editors. Wildland fire in ecosystems: effects of fire on soils and water. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.

Saint-Germain, M., P. Drapeau, and C. Hébert. 2004. Xylophagous insect species composition and patterns of substratum use on fire-killed black spruce in central Quebec. Canadian Journal of Forest Research 685:677–685.

Santín, C., S. H. Doerr, E. S. Kane, C. A. Masiello, M. Ohlson, J. M. de la Rosa, C. M. Preston, and T. Dittmar. 2016. Towards a global assessment of pyrogenic carbon from vegetation fires. Global Change Biology 22:76–91.

Schneider, M. P. W., L. A. Pyle, K. L. Clark, W. C. Hockaday, C. A. Masiello, and M. W. I. Schmidt. 2013. Toward a “molecular thermometer” to estimate the charring temperature of wildland charcoals derived from different biomass sources. Environmental Science and Technology 47:11490–11495.

Schmidt. 2013. Toward a “molecular thermometer” to estimate the charring temperature of wildland charcoals derived from different biomass sources. Environmental Science and Technology 47:11490–11495.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. BioScience 54:661–676.

Schoennagel, T., M. G. Turner, and W. H. Romme. 2003. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. Ecology 84:2967–2978.

Schoennagel, T., T. T. Veblen, J. F. Negron, and J. M. Smith. 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE 7:1–14.

Seidl, R., D. C. Donato, K. F. Raffa, and M. G. Turner. 2016. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. Proceedings of the National Academy of Sciences 113:13075–13080.

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

Stralberg, D., X. Wang, M.-A. Parisien, F.-N. Robinne, P. Sólymos, C. L. Mahon, S. E. Nielsen, and E. M. Bayne. 2018. Wildfire-mediated vegetation change in boreal forests of Alberta, Canada. Ecosphere 9:e02156.

Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.

Steventon, J. D. 2001. Morice Timber Supply Area Timber Supply Review. Smithers, British Columbia, British Columbia.

Stockstad, D. S. 1975. Spontaneous and piloted ignition of pine needles. Ogden, Utah.

Stockstad, D. S. 1979. Spontaneous and Piloted Ignition of Rotten Wood. Ogden, Utah.

Stuart, J. D., J. K. Agee, and R. I. Gara. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. Canadian Journal of Forest Research 19:1096–1104.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.

Swift, R. S. 2001. Sequestration of carbon by soil. Soil Science 166:858–871.

Talucci, A. C. 2019. Data and code: Outbreak and Wildfire Severity BC (Version v1.0.0) [Data set]. Ecosphere. Zenodo. http://doi.org/10.5281/zenodo.2648051

Talucci, A. C., and M. A. Krawchuk. 2019. Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. Ecosphere 10(5):e02744. 10.1002/ecs2.2744

Talucci, A. C., K. P. Lertzman, and M. A. Krawchuk. (2019). Drivers of lodgepole pine recruitment across a gradient of bark beetle outbreaks and wildfire in British Columbia. Forest Ecology and Management, *in review*. [This dissertation, Chapter 3]

Talucci, A. C. (2019). Data and Code: Recruitment after beetle outbreaks and wildfires (Version v0.1) [Data set]. Zenodo. http://doi.org/10.5281/zenodo.3235807 [This dissertation, Chapter 3]

Talucci, A. C. (2019). Data and Code: Beetles and fire landscape-scale BC (Version v0.1) [Data set]. Zenodo. http://doi.org/10.5281/zenodo.3235811[This dissertation, Chapter 4]

Talucci, A. C. (2019). Data and code: Pyrogenic Carbon (Version v0.1) [Data set]. Zenodo. http://doi.org/10.5281/zenodo.3235815 [This dissertation, Chapter 5]

Teste, F. P., V. J. Lieffers, and S. M. Landhäusser. 2011. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecological Applications 21:150–162.

Tinker, D. B., W. H. Romme, W. W. Hargrove, R. H. Gardner, and M. G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Canadian Journal of Forest Research 24:897–903.

Tinker, D. B., and D. H. Knight. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3:472–483.

Torn, M. S., P. M. Vitousek, and S. E. Trumbore. 2005. The influence of nutrient availability on soil organic matter turnover estimated by incubations and radiocarbon modeling. Ecosystems 8:352–372.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67:411–433.

VanDerWal, J., L. Falconi, S. Januchowski, L. Shoo, and C. Storlie. 2014. SDMTools: Species Distribution Modelling Tools: Tools for processing data associated with species distribution modeling exercises. R Packages version 3.4.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Springer, New York.

de Ville, N. 2013. Forest light and structure in relation to disturbances: comparing mountain pine beetle, wildfire, and salvage logging. Simon Fraser University.

Van Wagner, C. E. 1987. Development and structure of the Canadian forest fire weather index system. Forestry Technical Report 35. Ottawa.

Wagenbrenner, N. S., J. M. Forthofer, B. K. Lamb, K. S. Shannon, and B. W. Butler. 2016. Downscaling surface wind predictions from numerical weather prediction models in complex terrain with WindNinja. Atmospheric Chemistry and Physics 16:5229–5241.

Walck, J. L., S. N. Hidayati, K. W. Dixon, K. Thompson, and P. Poschlod. 2011. Climate change and plant regeneration from seed. Global Change Biology 17:2145–2161.

Walter, J. A., and R. V. Platt. 2013. Multi-temporal analysis reveals that predictors of mountain pine beetle infestation change during outbreak cycles. Forest Ecology and Management 302:308–318.

Walton, A. 2012. Provincial-level projection of the current mountain pine beetle outbreak: update of the infestation projection based on the 2010 provincial aerial overview of forest health and the BCMPB model (year 9). British Columbia Forest Service:1–15.

Wang, T., A. Hamann, D. L. Spittlehouse, and T. Q. Murdock. 2012. ClimateWNA—High-resolution spatial climate data for western North America. Journal of Applied Meteorology and Climatology 51:16–29.

Ward, A., C. A. Cansler, and A. J. Larson. 2017. Black Carbon on Coarse Woody Debris in Once- and Twice-Burned Mixed-Conifer Forest. Fire Ecology 13:143–147.

Wenger, K. F. 1984. Fire Management. Page 220 Forestry Handbook. John Wiley & Sons, New York.

Westfall, J., and T. Ebata. 2014. 2014 Summary of forest health conditions in British Columbia. Victoria, BC.

Wiedemeier, D. B., M. D. Hilf, R. H. Smittenberg, S. G. Haberle, M. W. I. Schmidt, W. D.B., H. M.D., S. R.H., H. S.G., and S. M.W.I. 2013. Improved assessment of pyrogenic carbon quantity and quality in environmental samples by high-performance liquid chromatography. Journal of Chromatography A 1304:246–250.

Wiedemeier, D. B., S. Q. Lang, M. Gierga, S. Abiven, S. M. Bernasconi, G. L. Früh-Green, I. Hajdas, U. M. Hanke, M. D. Hilf, C. P. McIntyre, M. P. W. Scheider, R. H. Smittenberg, L. Wacker, G. L. B. Wiesenberg, and M. W. I. Schmidt. 2016. Characterization, Quantification and Compound-specific Isotopic Analysis of Pyrogenic Carbon Using Benzene Polycarboxylic Acids (BPCA). Journal of Visualized Experiments:1–9.

Whitman, E., E. Batllori, M.-A. Parisien, C. Miller, J. D. Coop, M. A. Krawchuk, G. W. Chong, and S. L. Haire. 2015. The climate space of fire regimes in north-western North America. Journal of Biogeography 42:1736–1749.

Whitman, E., M.-A. Parisien, D. K. Thompson, R. J. Hall, R. S. Skakun, and M. D. Flannigan. 2018. Variability and drivers of burn severity in the northwestern Canadian boreal forest. Ecosphere 9.

Wong, C., H. Sandmann, and B. Dorner. 2004. Historical Variability of Natural Disturbances in British Columbia: A Literature Review.

Wulder, M. a., C. C. Dymond, J. C. White, D. G. Leckie, and A. L. Carroll. 2006. Surveying mountain pine beetle damage of forests: A review of remote sensing opportunities. Forest Ecology and Management 221:27–41.

Wulder, M. A., J. C. White, D. Grills, T. Nelson, and N. C. Coops. 2009. Aerial overview survey of the mountain pine beetle epidemic in British Columbia: Communication of impacts. BC Journal of Ecosystems and Management 10:45–58.