

**FIRE-RESILIENT ECOSYSTEMS: FIRE EXCLUSION AND SELECTIVE
HARVESTING DEGRADE DRY FORESTS IN BRITISH COLUMBIA**

by

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Abstract

In dry forests of southeastern British Columbia (BC) dense stands may be legacies of past high-severity fires and exist within the historical range of variability, or they may result from disruptions to historical fire regimes and indicate lost resilience. I conducted three dendrochronological studies that reconstructed the historical fire regimes and dynamics of these forests to discern the origin of high tree densities and guide ecosystem restoration to enhance forest resilience to fire and climate change. Historically, all 20 study stands were under an Indigenous-influenced, frequent, lower-severity fire regime. Moderate-severity fires initiated contemporary subcanopy cohorts, but ensuing fires, harvesting, and climate interacted to facilitate high tree densities. Fire exclusion prevented subsequent fires and allowed high densities to persist through time. In contrast to contemporary dense forests, historical stands were low-density and comprised of large, fire-tolerant trees; shade-intolerant ponderosa pine (*Pinus ponderosa*) and western larch (*Larix occidentalis*) dominated stand basal area. Historical selective harvesting removed the largest trees and favored shade-intolerant species. Contemporary stands are dominated by shade-tolerant Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), with 1407% more trees, 143% more basal area, and 63% smaller quadratic mean diameter than historical stands. Western larch regeneration is absent and ponderosa pine regeneration is negligible. All contemporary trees are stressed: growth rates have declined, missing rings have increased, and many trees are dying. Canopy-dominant trees are more stressed than trees in lower canopy positions, most likely caused by competition with suppressed trees for soil moisture. Western larch was most stressed while Douglas-fir was least stressed, owing to differences in life history attributes. Dense stands are artefacts of human exclusion of

fire and alterations to historical stand structures and composition, and represent degraded components of the dry forest matrix. To enhance resilience to fire and climate change, proactive forest management by thinning subcanopy trees will alleviate intense competition for soil moisture. Stands containing western larch should be prioritized to ensure its long-term persistence. Reintroducing fire provides necessary ecological feedbacks that will maintain resilience through time. Prescribed fires must be consistent with the reconstructed variation in historical frequency and severity, and will be enhanced by Indigenous knowledge.

Lay Summary

Dense forests are a concern in dry ecosystems because they increase the potential for crown fires that threaten human lives and infrastructure. Thinning dense forests reduces crown fire potential, but may remove variability in forests and reduce habitat for some wildlife species. My research refutes the idea that historically dense forests and crown fires were common in dry forests of southeastern British Columbia. My tree-ring reconstructions show frequent surface fires influenced by Indigenous people maintained open forests of ponderosa pine, western larch, and Douglas-fir. Over the 20th century, selectively harvesting large, fire-resistant trees, preventing Indigenous people from using fire in traditional ways, and suppressing fires allowed dry forests to become uncharacteristically dense. High tree densities have increased forest-wide stress and vulnerability to fire and climate change. Thinning subcanopy trees and prescribed surface fires are required to ensure the longevity and resilience of dry forests in southeastern British Columbia.

Preface

Gregory Greene was the main contributor to the identification, design, field research, sample processing, analyses and writing of this PhD dissertation. The thesis was supported throughout by Drs. Lori Daniels, Sarah Gergel, and Ze'ev Gedalof. Field methods for sampling sub-dominant trees in nested sub-plots were co-developed by Dr. Lori Daniels and Gregory Greene. All data are original and were obtained from field research conducted in the southern Rocky Mountain Trench of British Columbia, Canada, in 2013, 2014 and 2016. Assistance with field research was provided by Hans Erasmus, Ashley Dobko, Mylène Labonté, Zach Wentz, Vince Luu, Alex Pogue, Rodrigo Baston, Garrett Knochenmus, Dan Hornsberger and Javier Heredia. Assistance with sample preparation was provided by Dr. Raphael Chavardès, Eileen Xu, Jenny Liu, Ingrid Jarvis and 28 student volunteers from the University of British Columbia Conservation Integrated Field School course. Supporting contributions were provided by Kelsey-Copes Gerbitz (friendly review of complete dissertation) and Dr. Adam Polinko (friendly review of Chapter 4).

Table of Contents

Abstract.....	iii
Lay Summary	v
Preface.....	vi
Table of Contents	vii
List of Tables	xii
List of Figures.....	xiv
List of Abbreviations	xvi
Acknowledgements	xvii
Dedication	xix
Chapter 1: Introduction	1
1.1 Fire regimes at a cross-roads of interpretation.....	1
1.2 Urgent need for reconstructions of dry forest dynamics and fire history	4
1.3 The study system in southeastern British Columbia.....	5
1.4 Knowledge gaps in southeastern British Columbia	8
1.5 Scope of dissertation	9
1.6 Figures.....	11
Chapter 2: Low-severity fire regimes disrupted by forest harvesting and fire exclusion	
explain dense dry forests in British Columbia	12
2.1 Introduction.....	12
2.2 Methods.....	16
2.2.1 Research design and site selection	16

2.2.2	Stand structure and composition	17
2.2.3	Stand disturbance history and demography	18
2.2.4	Disturbance interactions and cohort dynamics	22
2.3	Results.....	24
2.3.1	Stand structure and composition.....	24
2.3.2	Stand disturbance history	24
2.3.3	Stand demography	26
2.3.4	Disturbance interactions drive cohort dynamics.....	28
2.4	Discussion	30
2.4.1	Low-severity fire regime was predominant	30
2.4.2	Disturbance interactions drive cohort initiation, facilitation, and persistence	32
2.4.3	European settlement disrupted the historical fire regime	35
2.5	Conclusions.....	36
2.6	Tables.....	38
2.7	Figures.....	42
Chapter 3: Harvesting and fire exclusion altered the resilience trajectories of dense dry forests in British Columbia		46
3.1	Introduction.....	46
3.2	Methods.....	49
3.2.1	Study area and research design	49
3.2.2	Harvest and fire history.....	49
3.2.3	Stand structure and composition.....	50
3.2.4	Dendrochronological reconstructions of disturbances and forest structures	51

3.2.5	Defining harvesting periods.....	53
3.2.6	Inferring fire exclusion	54
3.2.7	Temporal changes in stand structure, composition, regeneration, and mortality	54
3.2.8	Assessing departures from the Historical Range of Variability.....	56
3.3	Results.....	57
3.3.1	Harvest and fire histories	57
3.3.2	Stand structure and composition.....	58
3.3.3	Regeneration and mortality.....	59
3.3.4	Reconstructed harvesting.....	61
3.3.5	Inferred fire exclusion.....	62
3.3.6	Stand changes through time	62
3.3.7	Departures from the Historical Range of Variability (HRV).....	63
3.4	Discussion.....	64
3.4.1	Temporal trends align with other forests in western North America.....	65
3.4.2	Harvesting and fire exclusion interacted to create dense stands.....	68
3.4.3	All contemporary stands exceed the Historical Range of Variability (HRV)	70
3.4.4	Trends in regeneration and tree mortality indicate low resilience.....	71
3.5	Conclusions.....	73
3.6	Tables.....	74
3.7	Figures.....	80
Chapter 4: Sub-canopy trees outcompete canopy-dominant trees in dense dry forests of British Columbia.....		87
4.1	Introduction.....	87

4.2	Methods.....	90
4.2.1	Study area and research design	90
4.2.2	Data collection	90
4.2.3	Dendrochronological analyses	91
4.2.4	Stand structure, composition, and stage of stand development	92
4.2.5	Indicators of stress among height classes and species	93
4.2.6	Potential drivers and thresholds of stress in canopy dominant trees	95
4.3	Results.....	96
4.3.1	Stand Structure, Composition and Stage of Development.....	96
4.3.2	Indicators of Stress Among Height Classes.....	98
4.3.3	Indicators of Stress Among Species	99
4.3.4	Drivers and Thresholds of Stress in Canopy-Dominant Trees	100
4.4	Discussion	103
4.4.1	Stress in canopy-dominant trees	104
4.4.2	How are sub-dominant trees outcompeting canopy dominant trees?	106
4.4.3	Stress is driven by competition more than climate	109
4.5	Conclusions.....	111
4.6	Tables	112
4.7	Figures.....	115
	Chapter 5: Conclusion.....	122
5.1	Research contributions.....	122
5.2	Summary and main findings	123
5.3	Implications for dry forest management and restoration	126

5.4	Directions for future research	129
5.5	Figures.....	131
References		132
Appendices.....		161
	Appendix A.....	161
	Appendix B	162
	Appendix C	163
	Appendix D.....	164
	Appendix E	165
	Appendix F.....	166
	Appendix G	167
	Appendix H.....	168
	Appendix I	169
	Appendix J	170
	Appendix K.....	171
	Appendix L	172

List of Tables

Table 2.1 Composition, structure and harvesting impacts on the 20 study stands in the Ponderosa Pine (PP) and Interior Douglas-fir (IDF) zones of the southern Rocky Mountain Trench.	38
Table 2.2 Disturbance history of the 20 study stands.	39
Table 2.3 Factors contributing to cohort initiation, facilitation, and persistence.	40
Table 2.4 Sequences of disturbances in each plot and the percent of canopy and subcanopy tree establishment during cohort facilitation periods.	41
Table 3.1 Summary of stump surveys and harvest reconstructions in 20 plots in dense forests in southeastern BC.	74
Table 3.2 Fire history derived from plot-level fire-scar records.	75
Table 3.3 Plot-level stand structures for Period 1, Period 2 and Contemporary forests.	76
Table 3.4 Comparisons of stand structures in Period 1 (P1), Period 2 (P2) and contemporary (C) forests.	77
Table 3.5 Assessment of departures from the historical range of variation (HRV) of stand structures and species composition for plots stratified by composition.	78
Table 3.6 The types, limitations, and application of different methods of log skidding and transportation in the study area.	79
Table 4.1 Stand density, basal area (BA) and quadratic mean diameter (QMD) for the 20 study plots.	112
Table 4.2 Ages, growth rates and missing rings for the dominant tree species.	113

Table 4.3 Segments, slopes and breakpoints detected in standardized basal area increment	
chronologies and climate variables with segmented regression analysis, from 1928-	
2012.....	114

List of Figures

Figure 1.1 Twenty study plots represent dense (>25% canopy cover, and >400 live trees ≥ 12.5 cm dbh or >800 live and dead trees >1.3 m height ha ⁻¹) Douglas-fir, ponderosa pine and/or western larch stands in the dry, valley-bottom forests of the Rocky Mountain Trench in southeastern British Columbia, Canada.	11
Figure 2.1 Chronologies of (a) fire occurrence, (b & c) tree establishment in the Ponderosa Pine (PP) and Interior Douglas-fir (IDF) biogeoclimatic zones, and (d) reconstructed Palmer Drought Severity Index (PDSI; Cook <i>et al.</i> 2008).	42
Figure 2.2 Stand demography, disturbance history, and sample depth (number per year) of legacy trees in seven plots representing dense stands in the Ponderosa Pine (PP) biogeoclimatic zone. Canopy trees were in the dominant and co-dominant height classes; subcanopy trees were in the intermediate and suppressed height classes.	43
Figure 2.3a Stand demography, disturbance history, and sample depth (number per year) of legacy trees in seven plots (2-8) representing dense stands in the Interior Douglas-fir (IDF) biogeoclimatic zone. Canopy trees were in the dominant and co-dominant height classes; subcanopy trees were in the intermediate and suppressed height classes.	44
Figure 2.3b Stand demography, disturbance history, and sample depth (number per year) of legacy trees in six plots (9-14) representing dense stands in the Interior Douglas-fir (IDF) biogeoclimatic zone. Canopy trees were in the dominant and co-dominant height classes; subcanopy trees were in the intermediate and suppressed height classes.	45

Figure 3.1a Changes through time in the density of trees by size class in PP Plots.	80
Figure 3.1b Changes through time in the density of trees by size class in IDF Plots. Along the x-axis, time periods are within size classes.....	81
Figure 3.2a Changes through time in the basal area of trees by size class in PP Plots. Along the x-axis, time periods are within size classes.	82
Figure 3.2b Changes through time in the basal area of trees by size class in IDF Plots. Along the x-axis, time periods are within size classes.	83
Figure 3.3 Distribution of the density of dead trees across size classes in contemporary stands.	84
Figure 3.4 Changes in the distribution of stand-level basal area of live trees across size classes through time.	85
Figure 3.5 Historical range of variability of dry forests stands and changes through time following European settlement.	86
Figure 4.1 Assessment of self-thinning and stage of stand development.	115
Figure 4.2 Indicators of stress among trees stratified by height class.	116
Figure 4.3 Indicators of stress among canopy-dominant trees stratified by species.	117
Figure 4.4 Climatic trends for the study area (1928–2012).	118
Figure 4.5 Species-specific growth rates of canopy-dominant trees relative to stand structure (1928-2012).....	119
Figure 4.6 Relations between climate and indicators of stress among canopy-dominant trees by species.	120
Figure 4.7 Indicators of stress relative to stand structure among canopy-dominant trees by species.	121
Figure 5.1 Visual synthesis of findings from Chapters 2 and 3.....	131

List of Abbreviations

ASDI – Additive Stand Density Index

BA – Basal area

BAI – Basal area increment

BC – British Columbia

DBH – Diameter at breast height

HRV – Historical Range of Variability

NDT – Natural Disturbance Type

PDSI – Palmer Drought Severity Index

QMD – Quadratic mean diameter

RMT – southern Rocky Mountain Trench

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Dedication

I dedicate this dissertation to my loving partner, Kelly, and our amazing children, Ryder, Carter, Kamrynne, Madelynne and Piper.

Chapter 1: Introduction

1.1 Fire regimes at a cross-roads of interpretation

Forested ecosystems are quickly transforming in response to human and environmental drivers. Altered natural disturbance regimes due to forest management and land-use practices, compounded by ongoing climate change, are key factors contributing to this rapid change (Westerling *et al.* 2006, Carnicer *et al.* 2011, Williams *et al.* 2013, Hessburg *et al.* 2019, Anderegg *et al.* 2020). For example, between 1960 and 1995, forest harvesting in Canada replaced fire as the dominant disturbance in productive forests; more than 60% of Canadian forests are under forest tenure or within 10 km of a development (World Resource Institute 2000). Urban and industrial development and, thus, the wildland-human interface have also increased in forested landscapes. In Canada, at least 20.7% of the total wildland fuel area (i.e., the burnable portion of total land area) currently resides in the wildland-human interface, including urban (5.8%), industrial (1.9%), and infrastructure (19.5%) interfaces (Johnston and Flannigan 2018). Human-driven changes result in simplified but fragmented landscapes with reduced biodiversity, reduced habitat connectivity, and degraded resilience to disturbance (McIntyre and Barrett 1992, McIntyre and Hobbs 1999, Thompson *et al.* 2016). Changing climate exacerbates these issues through altered forest productivity (Boisvenue and Running 2006, Huang *et al.* 2010), inducing mortality in trees due to physiological stress (van Mantgem *et al.* 2009; Allen *et al.* 2010, Williams *et al.* 2013, Allen *et al.* 2015, Goulden and Bales 2019), and facilitating other landscape-scale processes including fire and insect outbreaks (Westerling *et al.* 2006, Raffa *et al.* 2008, Bentz *et al.* 2010, Falk *et al.* 2011, Higuera *et al.* 2015, McKenzie and Littell 2017, Holden *et al.* 2018, Littell *et al.* 2018). The cumulative impacts on disturbance

regimes and forests are expected to be even more pronounced in the coming decades as the climate continues to warm (Daniels *et al.* 2011, Schoennagel *et al.* 2017, Tepley *et al.* 2017, Miller *et al.* 2018, Serra-Diaz *et al.* 2018, Skinner *et al.* 2018, Coogan *et al.* 2021).

Changes to fire regimes can have dire consequences for the resilience of fire-prone ecosystems. In the dry forests that extend across western North America, fire is likely the most important disturbance agent. Dry forests are thought to have experienced a preponderance of frequent low- and moderate-severity surface fires prior to European settlement (Heyerdahl *et al.* 2001, Taylor and Skinner 2003, Falk 2004, Hessler *et al.* 2004, Wright and Agee 2004, Heyerdahl *et al.* 2007, Heyerdahl *et al.* 2012, Fulé *et al.* 2013, Hessburg *et al.* 2019), although high-severity, stand-replacing fires occurred in small, isolated areas (e.g., in patches from 1-100ha, Swetnam *et al.* 2011; at scales of <5% of the landscape, Brown *et al.* 2008). These frequent, lower-severity surface fire regimes maintained open-canopied, fire-resistant forest structures and compositions, which reinforced dry forest resilience to fires (Hessburg *et al.* 2019). However, the occurrence of fire has become much less frequent due to 19th, 20th and 21st century land use (e.g., urban development, farmland conversion, livestock grazing) and fire exclusion policies, including fire suppression and the prevention of Indigenous fire stewardship. Indigenous fires, in particular, were highly influential in driving the timing, frequency, location, and size of historical fires in utilized areas (Arno *et al.* 1995a, Keane *et al.* 2002, Turner *et al.* 2003, Bowman *et al.* 2011, Lake and Christianson 2019, Roos *et al.* 2021). Consequently, fire exclusion has driven landscape-scale changes to forest structure and composition, which has increased dry forest susceptibility to high-severity, stand-replacing fires (Hessburg *et al.* 2019).

Fire exclusion alters the structure and composition of dry forests by facilitating the establishment and persistence of subcanopy trees and promoting densely-stocked stands. The

effects of fire exclusion are evidenced by increased stand densities, decreased average tree size, a more complex canopy strata with abundant ladder fuels, an increase in shade-tolerant tree species, deeper layers of needle cast, a decrease in grass cover, slower nutrient cycling, and an overall decrease in forest biodiversity (Covington and Moore 1994a,b, Arno *et al.* 1995b, Fulé *et al.* 1997, Hessburg *et al.* 1999, Keane *et al.* 2002, MacKenzie *et al.* 2004, DeLuca and Sala 2006, Brown 2010). Fire exclusion can also promote forest encroachment into adjacent non-forest ecosystems, thereby reducing the size and biodiversity of other ecosystems (Arno and Gruell 1986, Turner and Krannitz 2001, Moore and Huffman 2004, Heyerdahl *et al.* 2006). These structural and compositional changes homogenize dry forests (Perry *et al.* 2011, Hessburg *et al.* 2019); the forest canopy becomes a vertically and horizontally contiguous fuel load that increases crown fire potential at the stand level (Brown 2010) and augments both the size and severity of fires across dry forest landscapes (Fulé *et al.* 2004).

Densely-stocked stands are the primary targets of ecosystem restoration treatments that aim to enhance fire resilience under a lower-severity fire regime. Contemporary forest management paradigms view dense stands as novel, degraded components of the dry forest matrix that are the consequence of fire exclusion. Restoration strategies under this paradigm are designed to mimic a frequent, lower-severity surface fire regime that is closely aligned with historical dry forest structure, composition, and function (Goldblum and Veblen 1992, Swetnam and Baisan 1996, Fulé *et al.* 1997, Allen *et al.* 2002, Agee 2002, Friederici 2003, Hessburg and Agee 2003, Hessburg *et al.* 2005). As a result, restoration treatments focus on thinning subcanopy trees and setting low-intensity fires to restore open, fire-resistant stand structures comprised of large, thick-barked, fire-tolerant trees (Kalies and Yocom Kent 2016, Hessburg *et al.* 2019, Stephens *et al.* 2021).

A lineage of recent research suggests that dry forests were historically dominated by mixed-severity fire regimes (Ehle and Baker 2003, Baker *et al.* 2007, Sherriff and Veblen 2007, Klenner *et al.* 2008, Williams and Baker 2012, Odion *et al.* 2014, Baker 2015, Hanson and Odion 2016). Mixed-severity fire regimes include a range of fire behaviors and effects across space and time, from low-severity surface fires to high-severity crown fires (Lertzman *et al.* 1998, Schoennagel *et al.* 2004, Daniels *et al.* 2017). The mix of fire severities produces a heterogeneous patchwork of open and closed forest structures across the landscape (Schoennagel *et al.* 2004, Baker *et al.* 2007, Hessburg *et al.* 2007). Although there is a long-standing debate around the degree to which low-severity vs. high-severity fires played a role in dry forests (Hessburg *et al.* 2007 vs Baker *et al.* 2007, Heyerdahl *et al.* 2012 vs. Klenner *et al.* 2008, Fulé *et al.* 2013 vs Williams and Baker 2012, and Stevens *et al.* 2016 vs. Odion *et al.* 2014), the potential for a greater proportion of high-severity fire in dry forests may have long-term implications for forest management strategies based on natural disturbance regimes. For example, high stand densities may be characteristic features of forests under a mixed-severity fire regime, potentially negating much of the perceived impact of fire exclusion on dry forest ecosystems (Baker *et al.* 2007, Williams and Baker 2012, Odion *et al.* 2014). If mixed-severity fire regimes played a significant role in dry forests, current ecosystem restoration practices (e.g., forest thinning and prescribed fire) may be forcing forest structures outside their historical range of variability (Keane *et al.* 2009, Williams and Baker 2012, Hanson and Odion 2016).

1.2 Urgent need for reconstructions of dry forest dynamics and fire history

To determine where ecosystem restoration treatments are needed to enhance ecosystem resilience, defined as the ability of forests to absorb or withstand disturbances, then recover and reorganize without shifting to a different state (Holling 1973, Holling 1996, Resilience Alliance

2021), forest managers require a better understanding of ecosystem specific: (1) historical fire regimes of dry forest ecosystems, including the contributions of Indigenous fire stewardship; (2) effects of past forest management practices and fire exclusion policies on stand dynamics; and (3) sources and thresholds of tree stress in dry forests. Doing so will allow forest managers to identify vulnerable areas and formulate ecologically-based management strategies. However, while historical data are needed to identify the degree to which forests and disturbance processes have changed, management decisions informed by the past must also consider contemporary warming climate and other recent anthropogenic changes that may be creating novel conditions (Hessburg *et al.* 2019, Hagmann *et al.* 2021). Consequently, forest managers must use the past as a starting point, but proactive management actions that realign or adapt contemporary forests to predicted future conditions may be necessary to ensure forest resilience to future change (Hagmann *et al.* 2021, Prichard *et al.* 2021, Hessburg *et al.* 2021).

1.3 The study system in southeastern British Columbia

The southern Rocky Mountain Trench (RMT) is a large, faulted valley west of the Rocky Mountains, located in southeastern British Columbia (49°27'N, 115°30'W; **Fig. 1.1**). The 257,702 ha study area extends from the Montana border in the south to the headwaters of Columbia Lake in the north. Within the study area, the terrestrial (grassland & forested) land base (199,457 ha) is a heterogeneous mix of open range ($\leq 10\%$ tree crown closure, 28% land base), open forest ($>10\text{--}40\%$ tree crown closure, 37% land base) and closed forest ($>40\%$ tree crown closure, 35% land base). Elevations range from 738 to 1169 meters above sea level. The study area climate is continental, with warm dry summers and cold winters. Annual precipitation recorded by four weather stations in the study area (**Fig. 1.1**) averaged 362 mm from 1970 to 2018. Mean annual maximum and minimum temperatures were 31.5°C and -18.1°C,

respectively, for this same period. Modern lightning-ignited fires in the RMT occur primarily in July and August (84% of 942 ignitions from 1991–2012, Cranbrook Fire Zone; BC Wildfire Service unpublished data).

The study area includes the Kootenay variants of the dry hot subzone of the Ponderosa Pine zone (PPdh2; hereafter “PP”) and dry mild subzone of the Interior Douglas-Fir zone (IDFdm2; hereafter “IDF”), according to biogeoclimatic ecosystem classification (Meidinger and Pojar 1991; **Fig. 1.1**). These biogeoclimatic zones represent dry, valley bottom forest ecosystems and include the northern range limit of ponderosa pine (*Pinus ponderosa* Douglas ex Laws.) in the RMT. The PP zone contains a high proportion of open range and the driest open- and closed-canopy forests, while the IDF zone encompasses fewer rangeland and slightly more mesic forest types.

Most forest stands (89% of forested land base) are dominated by ponderosa pine, Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco var. *glauca* [Beissn.] Franco), and/or western larch (*Larix occidentalis* Nutt). These three species differ in their tolerance to shade and fire. Ponderosa pine and western larch are considered shade-intolerant species, whereas Douglas-fir is shade-tolerant (Hermann and Lavender 1990, Oliver and Ryker 1990, Schmidt and Shearer 1990, Klinka *et al.* 2003). Ponderosa pine and western larch are the most fire-tolerant species in the study area. Ponderosa pine has thick bark when young (Safford and Stevens 2016), and both ponderosa pine and western larch grow very thick bark and self-prune their lower limbs as they mature (Arno and Fischer 1995, Franklin and Bergman 2011). Moreover, the deciduous nature of western larch makes the species resistant to crown fires in dormant seasons. Douglas-fir has an intermediate sensitivity to fire; small trees have very thin bark whereas large trees have thick bark, but the species is more prone to crown fires than western larch or ponderosa pine

(Hermann and Lavender 1990, Klinka *et al.* 2003). Lodgepole pine (*Pinus contorta* Douglas Ex Loudon) infrequently occurs as a dominant or co-dominant in stands, primarily in the IDF zone. Rocky Mountain juniper (*Juniperus scopulorum*) occurs as a sub-dominant in the driest portions of the PP zone.

[illegible]

European settlement of the RMT began in the 1860s following a gold strike near Fort Steele (White 1988). The Canadian Pacific Railway (CPR) began constructing the B.C. Southern Railway in 1897 (Davidson 1899). The line connected Lethbridge, Alberta with Nelson, B.C., and was completed in 1898. The B.C. government granted CPR 8,094 ha of land for each 1.6 km of track it constructed (Cranbrook History Book Committee 2002, p.47). Over 15,000 km² of land were granted to build the 467 km B.C. Southern Railway (Cail 1956, p.291), most of which

was in the Kootenay mountain valleys. CPR used this land to cut as many as 25 million board feet of sawlogs a year for railway ties, trestles, stations, warehouses, boxcars, and telegraph cross arms (Drushka 1998, p.65). Several other mills and small lines were constructed between 1900 and 1922 to extract timber (Turner 2010, p.20). By 1930 nearly all large, easily accessible trees were cut and railroad construction declined (Turner 2010, p.47).

Fire exclusion policies in B.C. were first established in 1874 with the *Bush Fire Act* (Parminter 1981). Associated with these policies was the prevention of First Nations fire stewardship, and the forced settlement of First Nations on reserves (**Fig. 1.1**). Fire suppression became much more successful following the introduction of aerial fire suppression after World War II (Beck *et al.* 2005). The B.C. Wildfire Service has successfully maintained a decades long suppression rate, with 94% of all surface wildfires (ranks 1-4: intensity $\leq 4,000$ kW/m) contained by 10 am the day after discovery (BCWS 2021a).

The RMT is currently home to over 30,000 people, and more than 55% of dry forests in the study area form the wildland-urban interface (BCWS 2021b; **Fig. 1.1**). As such, these valley bottom ecosystems have experienced the greatest anthropogenic impacts, which places them at the greatest risk of ecosystem degradation. Consequently, homes and other burnable human-built assets are at a high risk of catastrophic fire. However, the proximity to human resources and population centers lends these ecosystems as ideal candidates for forest management projects to restore dry forests to productive and resilient states. These efforts have the added benefit of reducing the risk of fire to adjacent communities and infrastructure.

1.4 Knowledge gaps in southeastern British Columbia

The current state of fire-resilience of dry forests in the RMT remains largely unknown. Specifically, we lack empirical evidence to discern whether the historical fire regime was

predominantly (a) lower-severity, with most of the landscape experiencing frequent surface fires; or (b) mixed-severity, with a large portion of the landscape subject to high-severity crown fires. This has direct implications for the management of these ecosystems; it is unclear whether the mechanisms that reinforce fire-resilience have been degraded. We also do not understand the ecological role of densely-stocked stands within the dry forest matrix. Are they expected or novel components of dry forest ecosystems? Under the veil of a warming climate, the impact of dense stands on large, thick-barked, fire-tolerant trees is also unknown. Do dense subcanopies pose a risk to these critical components of fire resilience? These knowledge gaps limit our ability to assess the degree to which fire exclusion (i.e., fire suppression and the prevention of Indigenous fire stewardship) and past forest management practices (i.e., historical selective harvesting) are affecting the resilience of these ecosystems. For contemporary disturbance-based management practices, the potential for historical dry forests to have existed under a mixed-severity fire regime questions the legitimacy of where and how ecosystem restoration treatments are being applied.

1.5 Scope of dissertation

In this dissertation I present three separate dendrochronological studies to investigate and address these knowledge gaps. Utilizing a proportional, stratified-random sampling design, I sampled 20 dense dry Douglas-fir, ponderosa pine, and/or western larch stands (>25% crown closure, and >400 live trees ≥ 12.5 cm dbh, or >800 live and dead trees >1.3 m height ha⁻¹) throughout the RMT. I targeted dense stands because they are central to the fire-resilience debate between the differing perspectives of lower- and mixed-severity fire regimes. I used information from surveys (i.e., stand structure and composition, stump counts/sizes/species), and samples from live and dead trees to produce tree-ring reconstructions of fire history, harvest history, stand

age and size structures, stand composition, and growth rates of canopy and subcanopy trees. In the first study (Chapter 2), I reconstructed the historical fire regime, harvest history, and stand dynamics through time to discern the factors (i.e., disturbance types, sequences, and their interactions) that initiate, facilitate, or enable the persistence of dense stands, and determine if the fire regime has changed. Assessments were made in the context of fires occurring near traditional Ktunaxa settlements, as their influences undoubtedly shaped the historical fire regime. In the second study (Chapter 3), I reconstructed historical stand structures and composition prior to harvesting, and quantified (a) the number, size, and species of trees removed, (b) trends in regeneration and mortality, (c) stand changes through time, and (d) the historical range of variability of pre-harvest stand configurations. I used the stand reconstructions to derive historical baseline values and determine if contemporary stands reflect degraded or resilient components of the dry forest matrix. I focused on the interactive effects of fire exclusion and historical harvesting, how the targeted removal of large, shade-intolerant but fire-tolerant trees affected stand dynamics, and the implications of those choices on the trajectory of dry forest resilience. In the third study (Chapter 4), I compared growth rates of trees in different canopy positions to determine if high stand densities are negatively affecting the growth of large, canopy-dominant, fire-tolerant trees. Analyses were conducted in the context of stand dynamics and climate change over the past 100 years. Finally (Chapter 5), I synthesized the results of my empirical research to prioritize future research and provide guidance for the management of dry, mixed-conifer forests in southeastern BC.

1.6 Figures

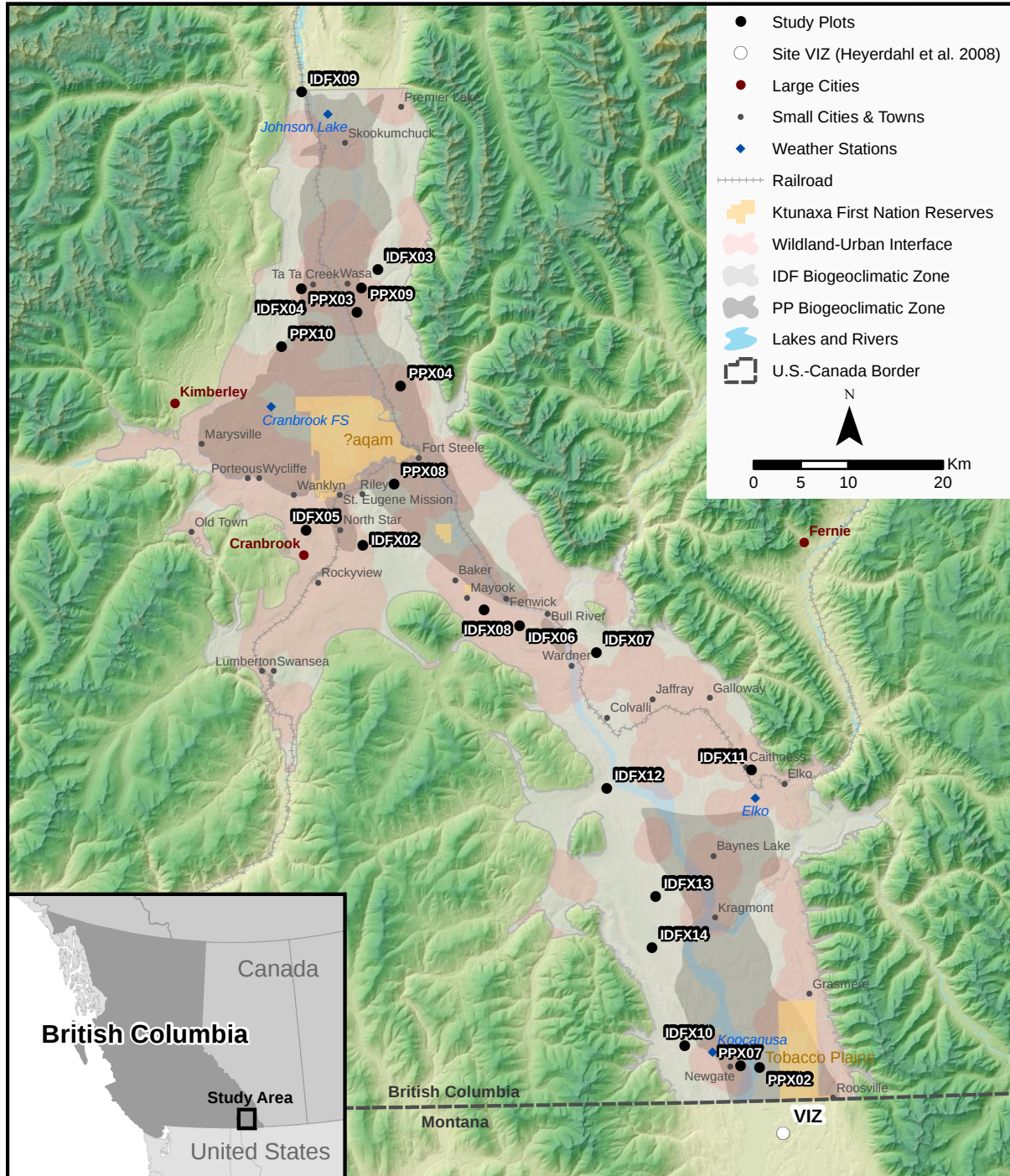


Figure 1.1 Twenty study plots represent dense ($>25\%$ canopy cover, and >400 live trees ≥ 12.5 cm dbh or >800 live and dead trees >1.3 m height ha^{-1}) Douglas-fir, ponderosa pine and/or western larch stands in the dry, valley-bottom forests of the Rocky Mountain Trench in southeastern British Columbia, Canada.

Of the 257,702 ha study area, 63% is in the Interior Douglas-Fir (IDF) and 37% is in the Ponderosa Pine (PP) biogeoclimatic zones.

Chapter 2: Low-severity fire regimes disrupted by forest harvesting and fire exclusion explain dense dry forests in British Columbia

2.1 Introduction

Past management combined with rapid changes in climate are altering the structure, composition, and function of forests, and promoting unprecedented wildfire and insect outbreaks, which further compromise the resilience of forests in western North America (Kurz *et al.* 2008, Abatzoglou and Williams 2016, Schoennagel *et al.* 2017, Serra-Diaz *et al.* 2018, Stephens *et al.* 2018, Hessburg *et al.* 2019). Ecosystem restoration is promoted as a proactive method to enhance forest resilience to climate change and disturbances (Hessburg *et al.* 2015, Stephens *et al.* 2021). Specific objectives vary, but the goal of ecosystem restoration is universal: assist with the recovery of an ecosystem that has been degraded, damaged, or destroyed (Gann *et al.* 2019).

In dry mixed-conifer forests, understanding of historical fire regimes greatly influences the perceived need for and type of restoration strategy to be employed. In the “low-severity” restoration model (Friederici 2003, Baker *et al.* 2007), dense forests are the consequence of fire exclusion, and restoration strategies mimic a lower-severity, surface fire regime that is closely aligned with historical dry forest structure, composition, and function. Within this model, dense stands are the primary targets for treatments that aim to thin understory trees and set low-intensity fires to restore open stands of fire-tolerant tree species (Kalies and Yocom Kent 2016, Hessburg *et al.* 2019, Stephens *et al.* 2021).

In contrast, the premise of “mixed-severity” restoration is that dense forests result from historical fire regimes that included low-, moderate-, and high-severity fires, which produce a heterogeneous patchwork of open and closed forest structures (Baker *et al.* 2007; Williams and

Baker 2012, Odion *et al.* 2014). In such mixed-severity landscapes, dense stands of even-aged cohorts are interpreted as those which are recovering from periodic high-severity crown fires. Such dense stands are thereby considered characteristic of the dry forest matrix and not in need of restoration (Baker *et al.* 2007; Williams and Baker 2012, 2014; Odion *et al.* 2014). Given these strongly contrasting perceptions, there is much debate around the degree to which lower- versus high-severity fires played a role in these ecosystems (Stevens *et al.* 2016 vs. Odion *et al.* 2014).

Anthropogenic activities also interact with fire to cultivate high density stands in some dry forests. In the case of Indigenous fire stewardship, there is growing recognition that influences on historical fire regimes have been overlooked and are underrepresented in historical forest fire research (Bowman *et al.* 2011). For millennia, burning by Indigenous people was performed to produce food, medicine, and culturally important plants, while fires for land clearing and habitat maintenance improved hunting and visibility (Lewis and Ferguson 1988, Turner *et al.* 2000, Kimmerer and Lake 2001, Lake and Christianson 2019, Prichard *et al.* 2021). Fires were commonly ignited in resource abundant areas or locations near culturally important assets. Fires were set in valley bottoms, along travel corridors, and/or near communities, as well as set across broader regions as part of seasonal rounds of harvesting (Barrett and Arno 1982, Lewis and Ferguson 1988, Turner *et al.* 2000, DeWilde and Chapin III 2007, Swetnam *et al.* 2016, Whitehair *et al.* 2018, Lake and Christianson 2019, Roos *et al.* 2021).

In the case of European settlement in North America, Indigenous fire stewardship was largely prevented when reserves and residential schools were established through the Indian Appropriations Act of 1851 and the Indian Act of 1876 in the U.S. and Canada, respectively. Another impact of European settlement on fire regimes was historical selective harvest in

ponderosa pine (*Pinus ponderosa* Douglas ex Laws.), Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco), and mixed-conifer forests, which increased tree densities relative to pre-harvest conditions (Schubert 1974, Veblen and Lorenz 1986, Heidmann 1988, Smith and Arno 1999, Kaufmann *et al.* 2000, Naficy *et al.* 2010). Concomitantly, post-harvest slash increased the intensity and severity of subsequent fires (Graham *et al.* 1999, Harmon 2002, Stone *et al.* 2004), in turn facilitating establishment of dense stands. In combination, fire exclusion and harvesting interacted to homogenize stand structure and increase densities, leading to stands dominated by many small, fire-intolerant trees (Naficy *et al.* 2010).

Despite the need for research accounting for disturbance interactions that may facilitate dense forests (Paine *et al.* 1998, Naficy *et al.* 2010), most research on historical fire regimes is conducted in areas perceived to have minimal human influences. For example, areas of historical logging are commonly avoided to minimize human influences likely to have confounding effects on fire history and age structure reconstructions (Ehle and Baker 2003, Sherriff and Veblen 2006, Heyerdahl *et al.* 2012, Harvey *et al.* 2017). Avoiding such areas likely systematically under-samples the locations most suitable for human habitation (Tomscha and Gergel 2015), even though fire occurrence is higher near past/present communities than in remote areas (Barrett and Arno 1982, Turner *et al.* 2003, DeWilde and Chapin III 2007, Swetnam *et al.* 2016, Lake and Christianson 2019, Roos *et al.* 2021). Consequently, the factors creating dense stands are often assumed from outcomes of studies in remote landscapes, which do not adequately account for anthropogenic influences near settlements in productive valley bottoms. Furthermore, past Indigenous influences are assumed to be spatially limited and thus remain poorly understood (Bowman *et al.* 2011).

In British Columbia (BC), Canada, restoration strategies for dry forest ecosystems operate under the “low-severity model” (Gayton and Hansen 1998, Rocky Mountain Trench Ecosystem Restoration Program 2013). Many restoration projects (e.g., forest thinning and prescribed low-severity fires) strategically target locations near modern communities because such treatments can also benefit fire safety concerns at the wildland-human interface (as defined by Johnston and Flannigan 2018). However, Klenner *et al.* (2008) argue that mixed-severity fire regimes (which include many high-severity fires), were dominant historically in BC’s dry forests, thus challenging the rationale for forest restoration. If the high-severity component was more ubiquitous historically, then current restoration practices may shift portions of the dry forest matrix outside its historical range of variability (Keane *et al.* 2009; Williams and Baker 2012, 2014; Odion *et al.* 2014). While in agreement with the mixed-severity classification, multiple fire regime reconstructions have reported abundant lower-severity fires with rare high-severity fires (Heyerdahl *et al.* 2012; Marcoux *et al.* 2013; Harvey *et al.* 2017).

A more comprehensive understanding of fire regimes and forest dynamics in dry forests is needed to better account for human influences (especially near past and present communities), understand the interaction among multiple disturbances, and assess the legitimacy of contemporary restoration practices, especially in regards to dense forest stands. To address these knowledge gaps, I used tree-rings to reconstruct fire histories, harvest histories, and age structures by focusing on densely-stocked, mixed-conifer stands located in the valley bottom of the southern Rocky Mountain Trench of BC. Within the traditional territory of the Ktunaxa (ktunáχq) First Nation (Ktunaxa Nation 2021), European settlement began in the 1860s and today, 30,000 people currently reside in the valley (White 1988), where ranching and forest management are extensive. I asked two questions: (1) Was the historical fire regime best

characterized as a low- or mixed-severity regime? (2) What types and sequences of disturbances interacted to initiate, facilitate, or enable the persistence of high stand densities? Outcomes of this research provide valuable information on the origin of dense stands given the historical fire regime, which is essential for guiding evidence-based ecosystem restoration in dry forests.

2.2 Methods

2.2.1 Research design and site selection

This study was conducted in the 143,379 ha of dry, valley bottom forests in the southern Rocky Mountain Trench (RMT), located in southeastern British Columbia, Canada (Chapter 1). I used a stratified-random design to select 20 high density stands for sampling. Using a GIS, the study area was stratified by latitude ($n = 4$ areas from north to south) and BEC zone ($n = 2$, PP and IDF zones). I identified potential study stands using the 2012 British Columbia Vegetation Resource Inventory (VRI) dataset (BC VRI 2021) that summarizes attributes of stands, with candidate stands (area ≥ 1 ha) delineated based on crown closure, density and species composition. To ensure sampled stands represented the subset of dry forests that are considered by the BC Ecosystem Restoration Program for restoration treatments, 5,134 stands (79,532 ha or 55% of dry forests) with $>25\%$ canopy cover, canopies dominated by Douglas-fir, ponderosa pine and/or western larch, and densities of >400 live trees ≥ 12.5 cm dbh, or >800 live and dead trees >1.3 m height, were identified as potential study stands. These thresholds are used by the BC Ecosystem Restoration Program to identify stands where there is greater potential for tree cover to reduce surface light penetration and negatively affect the productivity of understory plants (A. Neal and B.J.R. Harris, *personal communication*, January 24, 2021). It must be noted that VRI data is considered accurate in terms of crown closure, but VRI tree density data only includes trees in the dominant, co-dominant and high intermediate crown positions, and excludes

shorter-statured trees. As a result, the potential study stands underrepresent the total number of stands that would be considered for treatment by the BC Ecosystem Restoration Program, which are also represented by this study. A subset of 304 stands, representing 12% of candidate dry forests in the study area, were surveyed in the field prior to sampling to ensure suitability. Suitable stands were those with high stocking densities (>400 live trees ≥ 12.5 cm dbh ha^{-1} , or >800 live and dead trees >1.3 m height ha^{-1}), little to no recent harvesting activity and no evidence of tree planting. These criteria excluded 188 stands that had been commercially harvested, had been recently thinned through the BC ecosystem restoration program, or had low stocking densities. However, all surveyed stands included fire-scarred trees, snags, logs or stumps and numerous large stumps in later stages of decay, indicating historical fires and harvesting. From the subset of 119 suitable stands, 5 stands were randomly selected from each latitude stratum such that 7 and 13 of the stands selected for sampling were in the PP and IDF zones, respectively, consistent with their relative proportions in the study area.

2.2.2 Stand structure and composition

One-hectare plots were established in homogeneous portions of stands. I sampled three points at the center, northern and southern edges of each plot and averaged the values to determine tree density by species and size class. At each point, trees were sampled using variable radius plots and a BAF 2 prism to ensure ≥ 10 trees with a diameter at breast height (dbh) ≥ 7.5 cm were included in each plot. In two stands that did not meet these criteria, five and seven trees were sampled with a BAF 2 prism at each point instead. All saplings (i.e., trees <7.5 cm dbh and >1.3 m height) were tallied within 5.64 m (0.01 ha) of plot center. I recorded the species, dbh (in cm), overstory layer (i.e., canopy = dominant and co-dominant crown classes; subcanopy = intermediate and suppressed crown classes) and condition (i.e., live or dead) of all trees.

2.2.3 Stand disturbance history and demography

To reconstruct the disturbance history of each stand using tree-ring analyses, I sampled fire-scarred living and dead trees, harvested stumps and overstory trees to determine their age. All fire-scarred live trees and remnant snags, stumps and logs were identified in each 1-ha plot. Using a chainsaw, a full or partial cross section was removed from at least 10 live or remnant trees that had the greatest number of visible, well-preserved scars. To reduce impacts on live trees and snags, I removed partial cross-sections whenever it was safe to do so (Cochrane and Daniels 2008). I recorded the species, condition (tree, snag, log or stump) and number of visible scars for each sample.

To reconstruct harvest history, I censused stumps in half of each 1-ha plot. The species of stump was determined from remnant bark on the stump or near the root collar, the color and texture of the sapwood and heartwood, patterns of wood decay and scent of remnant wood. I recorded (a) decay class (1-4), (b) presence of char on the bark or wood surface and (c) presence of fire-scar lobes. I measured stump height and diameter inside the bark to reconstruct pre-harvest dbh using species-specific equations (Omule and Kozak 1989). For excessively rotten stumps without remnant wood ($n = 2$), inside bark diameter was estimated from standing remnant bark that was embedded in the ground. To determine the years of harvest, I sampled up to 10 stumps per plot with intact bark and/or phloem present. Full or partial cross-sections were sampled from at least 3 stumps from each of decay classes 1–2 and decay classes 3–4 that were nearest to plot center, assuming they represented more recent and older harvests, respectively. Living stumps with regenerative tissues growing over or near the top of stumps (Bormann and Graham 1959) were prioritized as they yielded the most precise harvesting dates. Sampling in this manner facilitated the testing of hypotheses that recent harvesting targeted smaller trees in

efforts to thin forests and enhance forest growth, whereas older harvests represented the selective harvesting of larger trees. To assess hypotheses, I tested if (i) stump age (calculated as 2013 minus the year of the outermost ring) and (ii) reconstructed dbh differed by decay class (i.e., decay classes 1-2 vs 3-4). Diameter at breast height and age data were not normally distributed, so a Mann-Whitney Rank Sum test was used to assess differences ($\alpha = 0.05$; SYSTAT 2008).

To reconstruct forest demography, I censused all canopy dominant trees, those with crown tops extending ≥ 1 m above the general canopy, in each 1-ha plot and recorded species, dbh, and condition (live, dead). Trees in other height strata were sampled in subplots centered on 1–3 randomly selected canopy dominant trees of differing species per plot, with more subplots in stands with multiple species of canopy dominant trees. Canopy dominant trees of each species were pooled, randomly assigned a number, then rearranged and selected by increasing order. Subplots were placed such that a minimum of 10 trees of each species were sampled. However, two study plots were dropped from analyses, so subplot counts totaled 9 for ponderosa pine, 12 for Douglas-fir, and 11 for western larch. An 11.28 m-radius plot (0.04 ha) was placed around selected canopy dominant trees; in one stand with density $>21,000$ trees ha^{-1} , an 8m-radius plot was used. For each tree I recorded species, condition (live or dead), dbh and overstory layer (canopy or subcanopy). To determine establishment dates, I sampled all live and dead canopy dominant trees in the 1-ha plot, and the 10 nearest trees (live and dead) in each of four diameter classes (large mature: $\text{dbh} \geq 30$ cm, small mature: $12.5 \text{ cm} \leq \text{dbh} < 30$ cm, pole: $7.5 \text{ cm} \leq \text{dbh} < 12.5$ cm, sapling: $\text{dbh} < 7.5$ cm and height > 1.3 m) in each subplot. When excessively rotten trees were encountered in subplots, the next nearest tree in the same size class was selected for sampling. For each sampled tree ≥ 12.5 cm dbh I extracted two opposing cores from within 30 cm of the ground. Multiple cores were extracted from each side to ensure rings were within an

estimated 10 rings of pith. For poles and saplings, full cross-sections were cut within 10 cm of the ground. Sample height and diameter at sample height were recorded for all sampled trees.

All cores and unstable cross-sections were mounted on wooden supports, sanded with successively finer sandpaper to 600 grit and scanned at high resolution (1200 or 2400 dpi). The ring widths of all scanned images were measured and cross-dated using the computer programs CooRecorder and CDendro (v9.0, Cybis Elektronik 2018). Cross-sections from fire-scarred live and remnant trees and stumps were cross-dated to determine the calendar years of the inner- and outer-most rings, and the year and season of each fire scar (Dieterich and Swetnam 1984). Outer-ring dates on stumps indicated the year of harvest. Since lightning ignitions in the study area occur primarily in the summer or fall, I assigned scars along ring boundaries (i.e., dormant season scars) to the earlier of the two adjacent calendar years.

Plot-level fire intervals were computed by compositing fire dates from all fire-scarred samples in each plot into a single record (Dieterich 1980). I used the program *Fire History Analysis and Exploration System* (FHAES 2.0.2; Brewer *et al.* 2016) to calculate minimum, maximum, and mean fire return intervals from fire interval distributions that included all fire scars (e.g., all fires that scarred ≥ 1 tree). To compare metrics to other studies, I also calculated fire return intervals for fire dates recorded on (a) at least two trees in the study area, and (b) at least two trees in each plot. Since I was interested in examining fine-scale dynamics within stands, analyses were conducted using metrics calculated from all fire scars. Due to the potential for subsequent fires to remove evidence of older fire scars, I reported the length of the full fire scar record for each plot (i.e., the inner-most ring date of the oldest tree to the year of sampling or outer-most ring date), but calculated plot-level frequency statistics for the period beginning when sample depth included ≥ 3 trees per plot. I calculated the time since the last fire (TSLF) for

each plot as the number of years from the last fire to the year 2013 (i.e., the first year of sampling) and compared it to the plot-level maximum fire return interval.

To estimate years of tree establishment as accurately as possible, I used cross-dated pith or inner-ring dates. For the subset of increment cores that did not intercept the pith, a geometric correction was applied to estimate the number of missing rings (Duncan 1989). For all increment cores and disks, the number of years for trees to grow to sample height was determined by developing species-specific regressions (Villalba and Veblen 1997, Wong and Lertzman 2001). I sampled 35, 28, 12 and 18 regenerating Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco var. *glauca* [Beissn.] Franco), ponderosa pine (*Pinus ponderosa* Douglas ex Laws.), western larch (*Larix occidentalis* Nutt) and lodgepole pine (*Pinus contorta* Douglas ex Louden), respectively, that were 20–150 cm in height and grew in open conditions in 10 study plots. Individuals were uprooted or cut at the root-shoot interface and sectioned at 10 cm intervals. The resulting samples were sanded to 600 grit and ring counts were used to develop species-specific regressions of age (ring counts) on height that were applied to estimate the number of years to grow to sample height ($r^2 = 0.89\text{--}0.93$, SEE = 2.81–7.78 years, Appendix A). For each tree, its year of establishment was the inner-ring date minus the corrections for missed rings and sample height (Daniels *et al.* 2017).

To represent the origin and development of the contemporary stands, I calculated the number of sampled trees that established per year and converted them to the number of trees per hectare based on the densities measured in the stand composition and structure plots. The establishment of canopy and subcanopy trees were summarized in cumulative step curves. To allow comparison among canopy strata and stands with different densities, relative rather than absolute values were used in the curves.

I identified cohorts in the canopy and subcanopy strata as periods when $\geq 20\%$ of trees established within a 15-year period, preceded by at least 15 years during which trees from other cohorts did not establish. After testing windows from 10 to 20 years, the 15-year window was selected because it accounted for potential errors in tree-age estimates, as 92.5% of age corrections were ≤ 15 years, and minimized the number of windows with more than one fire year. I assigned the year of cohort initiation as the calendar year of establishment of the oldest tree in each cohort. I considered canopy and subcanopy cohorts to comprise a single, even-aged cohort if they established ≤ 15 years apart and assigned the initiation date of the oldest of the two cohorts as the final initiation date. Due to the potential for climate to promote tree establishment (Brown and Wu 2005), I assessed the average climatic conditions during the first 15-years of cohort establishment. Favorable conditions were indicated by relatively cool or wet climate, as reported by a tree-ring reconstruction of the summer Palmer Drought Severity Index (PDSI) (June-August, grid point 67; Cook *et al.* 2008).

2.2.4 Disturbance interactions and cohort dynamics

To infer disturbance history and forest dynamics, I used multiple lines of evidence including fire-scar and harvest dates, tree establishment and cohort dates in the contemporary stands, and the presence of veteran trees that survived at least one fire through time, determined from the legacy snags, logs and stumps. All plots included multiple fire scars and at least one cohort, meeting the criteria commonly used to define a mixed-severity fire regime (Daniels *et al.* 2017). This classification assumes that cohorts initiate following relatively high-severity fire, and their establishment and persistence reflects well-documented stand development processes rather than subsequent disturbance. To test this assumption, I aimed to: (1) distinguish historical high-versus moderate-severity fires and determine the severity of fires that initiated cohorts in each

plot; (2) determine if harvesting contributed to cohort initiation, and (3) determine if subsequent disturbances facilitated the establishment and persistence of the most recent cohort in each plot.

To infer the causes of cohort initiation, I compared each initiation date with the fire-scar and harvest dates in the same plots. While I recognize that cohorts can initiate following other disturbance types (e.g., insects, disease, windthrow), I did not find evidence of stand-wide disturbances other than fire and harvesting in my study plots. Each cohort was assessed to determine if it was initiated by a high- or moderate-severity fire, whether harvesting occurred prior to initiation, and the lags between fire and/or harvesting events and cohort initiation. High-severity fires were identified by cohorts that initiated in absence of fire scars and surviving trees, assuming the fire was intense enough to kill existing trees and consume fire-scar evidence. Moderate-severity fires scarred trees and generated cohorts, but veteran trees survived.

I assessed the most recent cohort in each plot to determine if subsequent disturbances may have facilitated cohort establishment and/or contributed to cohort persistence. Cohort facilitation was assessed during the period beginning with initiation of the most recent cohort and ending when stands reached their maximum contemporary densities. I considered this a period of facilitation because disturbances outside the 15-year window of cohort establishment likely augmented the duration and amount of recruitment into these cohorts. Cohort persistence was assessed during the period after stands reached their maximum contemporary densities. I considered this a period of persistence because, although disturbances occurred, they did not instigate tree recruitment into the canopy or subcanopy (i.e., stands were in the stem-exclusion stage of development; Oliver and Larson 1996). The factors considered were the number and sequence of subsequent fires and/or harvests, the lags between cohort initiation and those disturbances, and the average climatic conditions (i.e., PDSI) during the first 15-years of cohort

establishment. I also assessed the lags between cohort initiation and (a) the year that the last tree established in each stand, and (b) the year TSLF exceeded the longest reconstructed fire return interval.

Sequences of fires and/or harvests were assessed during each facilitation period and were grouped by alternating types of disturbances. I tested if the percent of canopy and subcanopy tree establishment in stands with harvest-fire sequences differed from stands with other sequences. Relative values of tree establishment were used to account for potential differences in site productivity among stands. Data were not normally distributed, so differences were assessed using a Mann-Whitney Rank Sum Test ($\alpha = 0.05$; SYSTAT 2008).

2.3 Results

2.3.1 Stand structure and composition

Stand densities ranged from 1,098–21,847 trees ha⁻¹ (**Tables 2.1, 2.2**). Within stands, canopy densities ranged from 79–590 trees ha⁻¹ ($\mu = 197$) and subcanopy densities ranged from 1,019–21,662 trees ha⁻¹ ($\mu = 4,084$). Subcanopy trees comprised 84–99% of each stand. Douglas-fir dominated the canopies of 13 stands and the subcanopies of 17 stands. Ponderosa pine occurred in 15 stands, but dominated or co-dominated canopies of only two stands. Similarly, western larch occurred in 12 stands, but dominated or co-dominated canopies in four stands. Lodgepole pine and Rocky Mountain juniper were present in five and two stands, respectively, but comprised <2% of stand densities.

2.3.2 Stand disturbance history

All plots contained numerous trees with visible fire-scars ($\mu = 17$ ha⁻¹, range 10–24); 20% had a single visible scar, and 80% had multiple visible scars ($\mu = 5.3$ tree⁻¹, range 2–38). I sampled a total of 213 fire scarred trees specifically for fire history reconstructions ($\mu = 11$ plot⁻¹,

range 10–17); an additional 35 harvest history samples with fire scars were included in fire regime analyses. Most samples were from western larch and ponderosa pine (44% and 46%, respectively), and the remainder were from Douglas-fir (10%). I dated 1,646 fire scars between 1207 and 1965, with an average of seven scars·sample⁻¹ (range 1–52). Dates composited at the plot-level yielded 623 fire events across the study area, with an average of 33 fires per plot (range 6–69) (**Fig. 2.1**). Nearly half of the fire events (49%) scarred ≥ 2 trees per plot, and ≥ 2 trees were scarred across the study area in 82% of fire years. Plot-level fire return intervals averaged 11.6 years for all scarred trees (range 7.0–14.9 years) during the period beginning when sample depth included at least three trees (**Tables 2.1, 2.2**). Over the same period, mean fire return intervals for when fires scarred ≥ 2 trees per plot and when ≥ 2 trees were scarred across the study area were 18.0 years (range 9.2–26.3) and 13.7 years (range 7.5–18.4), respectively. TSLF ranged from 48–140 years and exceeded the longest reconstructed fire return interval in all plots.

Plots contained an average density of 150 stumps·ha⁻¹ (range 18–330) (**Table 2.4**). Stumps were primarily Douglas-fir (61%), though numerous western larch (21%) and ponderosa pine (18%) stumps were present. Decay classes varied within plots, but most stumps were in classes 3 (69%) and 4 (18%). Diameter at breast height reconstructions indicated that most stumps were from large diameter trees (52% ≥ 30 cm dbh); 99% of large stumps were in decay classes 3 (76%) and 4 (23%).

I sampled a total of 133 stumps specifically to assess harvest dates (**Table 2.4**). These were supplemented by 24 fire scar samples from stumps that also had intact bark and/or phloem. Together, an average of 8 samples per plot (range 2–12) were used to assess harvest dates. Among the 20 plots, I identified 41 harvest years from outer ring dates and supplementary lines

of evidence (**Figs. 2.2–2.3**). I was unable to identify an exact harvest year from stump samples in PPX03; however, releases in adjacent canopy trees suggested a single harvest date of 1922. In IDFX12 most stump samples were from trees that were killed by a fire in 1918 that caused releases in adjacent trees. However, numerous stump tops in this plot were charred, indicating they were cut sometime after 1918 but before the final fire burned in 1926. Given this evidence, I assigned the first IDFX12 harvest date as 1919, one year following the death of many stump samples in the plot.

All harvesting occurred from 1907–1994, although 55% of harvest events were before 1956 (**Tables 2.1, 2.2; Figs 2.2–2.3**). Multiple harvest years (range 2–4) were identified in 12 plots; the first harvest occurred on or before 1919 in these plots. All stands had been harvested at least once by 1964, and 95% of harvesting took place before 1980. Mann-Whitney Rank Sum Tests indicated stumps in decay classes 1–2 were significantly younger (median age = 31 years; $P < 0.001$) and smaller (median dbh = 9.4 cm; $P < 0.001$) than stumps in decay classes 3–4 (median age = 94 years, median dbh = 39.8 cm).

2.3.3 Stand demography

I estimated the ages of 1,255 living trees and 218 dead trees, and used an average of 74 (range 44–132) tree ages per plot to derive contemporary age structures. Across the study area, individual trees established from 1388–1981 (**Fig. 2.1**); nearly all trees (90%) established between 1891–1950, but nearly half of trees (44%) established in a short 15-year period between 1896–1910. The oldest canopy trees established between 1388–1905, while the oldest subcanopy trees established between 1800–1931. Canopies were generally much older than subcanopies ($\mu_{\text{difference}} = 176$ years). However, two plots (i.e., IDFX08 and IDFX09) had canopies and

subcanopies that established within eight years of each other and had the youngest canopies (108 and 175 years, respectively).

Fifty cohorts were identified among the 20 plots, with 30 in canopies (range 1-3 per plot) and one in each subcanopy ($n = 20$) (**Figs. 2.2-2.3**). A total of 34 canopy and subcanopy cohorts (68% of cohorts) established ≤ 15 years apart, representing 17 single, even-aged cohorts. Cohort establishment dates ranged from 1630–1933, but most cohorts (72%) established in a 55-year period, from 1881–1935 (**Table 2.3**). Canopy cohorts contained an average of 98 trees ha^{-1} (range 27–258) and subcanopy cohorts contained an average of 2,950 trees ha^{-1} (range 210–21,662) (**Tables 2.1, 2.2**). Douglas-fir, ponderosa pine and western larch were present in 46, 23 and 18 cohorts, respectively. Lodgepole pine was present in three subcanopy cohorts, and comprised between 2%, 4% and 17% of each, but represented $<1\%$ of total cohort composition. Douglas-fir was most abundant in cohorts (84%), followed by western larch (9%) and ponderosa pine (7%). Cooler, wetter climate occurred during the first 15 years of establishment of 12 cohorts (**Table 2.3**). Seven of these initiated between 1892 and 1906, with subsequent tree establishment overlapping with the 15-year period between 1896–1910, when 44% of trees established in 16 plots. Of the 16 plots with tree establishment between 1896–1910, 11 had at least one fire or harvest event during the 15-year period, and the remaining five had at least one fire between 1886–1895, indicating establishment was not independent of disturbance.

Evidence from samples of legacy snags, logs and stumps revealed tree ages that pre-dated contemporary age structures in 75% of plots (**Figs. 2.2–2.3**). In PPX02, IDFX06, IDFX09, IDFX10 and IDFX11, the oldest contemporary live trees co-established within ± 14 years of the oldest legacy trees. Harvesting removed old trees from all plots and the oldest trees from 60% of plots. Combined evidence from legacy samples indicated the ages of old trees in each plot

spanned at least 170–720 years, and legacy trees pre-dated contemporary tree ages by an average of 322 years per plot (range 40–636 years; excluding PPX02, IDFX06, IDFX09, IDFX10, IDFX11).

2.3.4 Disturbance interactions drive cohort dynamics

All but one even-aged cohort established within an average of 5 years following moderate-severity fires (range 0–20 years) (**Table 2.3**). In IDFX09, the oldest canopy cohort initiated following a high-severity fire. Although absent in the contemporary live tree age structure, the establishment dates of legacy samples in IDFX03 suggested that harvesting removed a cohort that initiated following a high-severity fire (**Fig. 2.3a**). The first harvest events in PPX10 and IDFX12 occurred prior to initiation of the most recent cohort by 14 and 8 years, respectively.

Disturbances occurred after initiation of the most recent cohort in all plots (**Figs. 2.2–2.3**). Subsequent fires occurred in 12 plots ($n = 24$, range 1–4 fires per plot); 23 fires occurred during the facilitation period, and one fire, recorded on one tree in IDFX06, occurred during the persistence period. Subsequent harvesting occurred after initiation of the most recent cohort in all plots ($n = 40$, range 1–4 harvests per plot); 20 harvests occurred during the facilitation period, and 20 harvests occurred during the persistence period. PDSI values averaged over the 15-year period following cohort initiation indicated cool and/or wet climate occurred during establishment of eight of the most recent cohorts, between 1892 and 1921. The last tree established in each stand within an average of 36 years following initiation of the most recent cohort (range 17–76 years). TSLF exceeded the longest reconstructed fire return interval in eight plots during the facilitation period and in all plots during the persistence period. TSLF exceeded the longest reconstructed fire return interval in all plots within an average of 45 years following

initiation of the most recent cohort (range 21–73 years); 90% of plots were outside their historical range of variability by 1976. Had fires continued burning at their mean return intervals, an average of 9 additional fires (range 3–17) would have occurred in each plot.

Six distinct sequences of fire/harvest disturbances were identified among plots during the facilitation period (**Table 2.4**). These included: (1) fire only; (2) fire–harvest; (3) fire–harvest–fire; (4) harvest only; (5) harvest–fire; and (6) harvest–fire–harvest. The durations of facilitation periods generally increased commensurate with the percentage of canopy tree establishment. No disturbances occurred during the facilitation period in PPX10. This plot had the shortest facilitation period of 17 years and only 1% of canopy trees established in that time. Among plots with facilitating disturbances, those with fire-harvest sequences produced the lowest percentages of canopy tree recruitment (median = 13%) over a median duration of 28 years. In harvest only and fire only plots, 48% and 64% of canopy trees, respectively, established over a median duration of 30 years. In plots with harvest-fire sequences, 84% of canopy trees established over a median duration of 36 years. In plots with harvest-fire-harvest sequences, 90% of canopy trees established over a 51-year period. The two plots with fire-harvest-fire sequences had the highest percentages of canopy tree establishment (median = 96%) over a 49-year period; three consecutive fires occurred before the harvest in each of these plots.

A significantly higher percentage of canopy trees established in association with harvest-fire disturbances (median = 92.1% in sequences 3, 5, 6 above) than with other disturbance sequences (median = 42.1% in sequences 1, 2, 4 above; Mann-Whitney U-test = 8.000, $P = 0.007$). However, the percentage of subcanopy trees that established following the same groups of disturbance sequences were not significantly different (medians = 97.6% and 96.4% establishment, respectively; Mann-Whitney U-test = 32.000, $P > 0.05$).

2.4 Discussion

Tree-ring reconstructions of the historical fire regime and the drivers of high stand densities in dry valley-bottom forests in the RMT revealed four striking outcomes. (1) Multi-century fire scars showed few cohorts prior to 1900, indicating a low-severity fire regime was predominant (rather than mixed-severity). (2) Contemporary stands were dense because of recent cohorts that initiated following moderate- rather than high-severity fires, with confounding influences by early 20th century harvesting. (3) Once cohorts initiated, additional tree recruitment was facilitated by interactions between subsequent disturbances and climate. (4) Widespread fire exclusion during the 20th century enabled the persistence of dense stands through time. Next, I explain these findings in deeper detail and discuss the factors that influenced and disrupted the historical fire regime.

2.4.1 Low-severity fire regime was predominant

Low-severity fires dominated the reconstructed fire regime. Legacy stumps, snags and logs, embedded in contemporary high-density stands, revealed long-lived trees that survived at least 850 years of frequent low-severity fires prior to the 20th century. Alone, a ponderosa pine tree with 52 fire scars (the record for this species) clearly showed that frequent surface fires once prevailed in a stand that last burned in 1895 and now contains almost 2,000 trees ha⁻¹. Despite the northerly latitude of the RMT, short fire return intervals of 7 to 15 years within plots were comparable to intervals in mixed-conifer forests growing in dry climates of the southwestern United States (Swetnam and Baisan 1996, Brown *et al.* 2001, Johnson and Margolis 2019, Hessburg *et al.* 2019). Among fire history reconstructions in BC, dry forests in the RMT included longer-lived trees and shorter fire return intervals than previously reported (Daniels and Gedalof 2012, Heyerdahl *et al.* 2012, Marcoux *et al.* 2015, Greene and Daniels 2017, Harvey *et*

al. 2017), except Pogue (2017) who reported similar fire return intervals prior to European settlement in the Okanagan.

Several other fire history reconstructions in dry forests of BC have reported a preponderance of low-severity fires, although their historical regimes are generally classified as mixed-severity. Among other dry forests, fire-scarred but long-lived fire-tolerant trees yielded fire records up to 500 years and included relatively few cohort-generating events (ca. 11–25% of events) (Heyerdahl *et al.* 2007, 2012; Harvey *et al.* 2017). Persistent fire-scarred trees indicated low-severity fires were also common in mesic montane and some lower subalpine forests, although cohorts provided evidence of periodic moderate- and high-severity fires as well (Marcoux *et al.* 2013). Marcoux *et al.* (2015) and Greene and Daniels (2017) reconstructed mixed-severity fire regimes in montane forests that included fire records dating to 1270 and 1406 AD, respectively. Long-lived trees in lower elevation forests survived low- and moderate-severity fires every 7 to 56 years. In contrast, higher elevation forests consisted of even-aged cohorts that averaged 198 years in age (range 77–375 years), and were products of infrequent, high-severity fires. The potential loss of evidence of cohorts through subsequent disturbances makes it challenging to classify the severity of individual fires in the distant past (Daniels *et al.* 2017). Collectively, however, results from numerous studies clearly link tree longevity and persistence in dry and mesic forests of BC to frequent, lower-severity surface fires, and corroborate the conclusion that lower-severity fires dominated my study area. Had more high-severity fires occurred, shorter fire records would have been more common.

The multi-century fire-scar records of the RMT are partly attributed to a scarcity of stand-replacing fires, although periodic high-severity fires are expected in dry forests with low-severity fire regimes (Schoennagel *et al.* 2004, Swetnam *et al.* 2011, Fulé *et al.* 2013, Bakker *et al.* 2019).

Although each plot included at least one post-fire cohort, all but two cohorts established after a moderate-severity fire rather than a high-severity fire. The two high-severity fires ca. 211 and 175 years ago initiated two of the youngest study stands (IDFX03 and IDFX09). These two fires, identified by cohorts in absence of fire scars or veteran trees, represented $<0.3\%$ of recorded fires and suggest that $\leq 5\%$ of the study area burned at high severity in each of those two fire years. These results are within the range of variation of high-severity fires embedded in low-severity fire regimes in other dry forests. In the southwest United States, historical patches of high-severity fire have been documented at scales of 1–100 ha (Swetnam *et al.* 2011). In South Dakota and the Sierra Nevada mountains of California, high-severity fires historically burned $\leq 7\%$ of the total area of dry forest landscapes (Brown *et al.* 2008, Miller and Safford 2017). Moreover, the most recent cohort in each plot persisted during unprecedented fire-free periods of 48–140 years that exceeded historical mean fire intervals by a factor of 3 to 17. Thus, I conclude these cohorts were not indicative of rare high-severity fires within the historical fire regime, but exist due to anthropogenic disruptions to that fire regime during the 20th century.

2.4.2 Disturbance interactions drive cohort initiation, facilitation, and persistence

Recent cohorts were initiated by moderate-severity fires, with confounding influences by early 20th century harvesting. In each plot, the most recent cohort initiated within 20 years of a moderate-severity fire, although harvesting preceded fire in two plots (PPX10 and IDFX12) and followed fires in all plots. In the dry forests of BC, fires commonly drive cohort initiation (Heyerdahl *et al.* 2012, Marcoux *et al.* 2015, Harvey *et al.* 2017). Post-fire cohorts can initiate immediately or lag fires by as many as 30–50 years (Sherriff and Veblen 2006, Baker *et al.* 2007). Therefore, the observed cohort initiation within 20 years of fires is within the reported range of post-fire initiation. The harvesting that preceded the fires in plots PPX10 and IDFX12

likely had two effects on cohort initiation. First, removal of most overstory trees released growing space and reduced competition for light and resources (Oliver and Larson 1996). Second, late 19th and early 20th century harvesting routinely left slash and upper tree boles with attached branches on the ground, increasing surface fuel loads (Covington *et al.* 1994). The spread and intensity of post-harvest fires would have been augmented by these fuels, releasing additional growing space, exposing mineral soil, and enhancing the likelihood of a cohort initiating.

Fires initiated cohorts, but the type, severity, timing, and sequence of subsequent disturbances facilitated tree recruitment into the cohorts by generating additional growing space and suitable seedbeds. In general, where harvesting or fires followed cohort initiation, a higher proportion of trees established during the facilitation period than in plots with few or no subsequent disturbances. Moreover, the proportion of canopy tree recruitment increased commensurate with increasing complexity of disturbance interactions. For example, three consecutive fires at short intervals before harvesting in plots PPX04 and PPX09, and harvest-fire sequences in general, promoted the greatest proportions of canopy tree establishment within the post-disturbance cohort. Evidently, the proportion of tree establishment following cohort initiation was proportional to the amount and type of growing space released and the type of seedbeds produced by subsequent disturbances and their interactions.

The three fire-tolerant species that dominate the study area, ponderosa pine, western larch, and Douglas-fir, have high potential for natural regeneration following disturbance (Klinka *et al.* 2003). Ponderosa pine and western larch are shade-intolerant (Klinka *et al.* 2003), while all three species germinate best in exposed mineral soil or ash (Minore 1979) and are moderately to highly tolerant of heat and water deficits that occur in open post-disturbance environments

(Klinka *et al.* 2003). Compared with surface fires, harvesting releases more above-ground growing space by directly and immediately removing overstory trees, but exposure of mineral soil is limited to isolated patches (e.g., skidding locations; Cromack *et al.* 1978). Surface fires expose more mineral soil than harvesting due to the contiguous consumption of surface vegetation, litter, and soil organic matter, while ash is created by fire only. Mineral soil exposure and ash creation escalate with the severity of surface fires (Certini 2005), particularly when consecutive fires burn at short intervals or fire follows harvesting. The cumulative effects of repeat surface fires interacting with harvesting in the early 20th century facilitated the densest stands in the RMT, with up to 590 canopy trees ha⁻¹ and 1,020 to 21,660 subcanopy trees ha⁻¹.

Climatic variation concurrent with fires and harvesting also facilitated cohorts. During 15 years of relatively wet, cool climate from 1896–1910, nearly half the trees in the study and eight of the most recent cohorts established. Similarly, Brown and Wu (2005) identified a distinct period of ponderosa pine regeneration across their dry study area in South Dakota. They attributed the widespread cohort initiation to optimal climatic conditions for tree establishment, independent of disturbance. In contrast, all recent cohorts in my study were facilitated by subsequent fires or harvesting, augmented by climate.

The exclusion of lower-severity fire explains cohort persistence in the dense stands of the RMT. Fire exclusion removed the primary mechanism for maintaining low tree densities, since frequent lower-severity fires kill small, thin-barked trees, thereby limiting tree regeneration and recruitment to canopy strata (Hessburg *et al.* 2005). High densities of shade-tolerant but fire-intolerant trees are a common trend following fire exclusion from dry forests across western North America (Keane *et al.* 2002, Naficy *et al.* 2010, Merschel *et al.* 2014, Harris and Taylor 2015). In the dense stands of the RMT, contemporary subcanopies are dominated by thousands

(e.g., 1,020 to 21,660 per ha) of small, thin-barked Douglas-fir. Had lower-severity fires continued at historical mean return intervals, an average of eight fires (range = 3-17) would have burned each stand, undoubtedly killing most subcanopy Douglas-fir and dramatically reducing stand densities.

2.4.3 European settlement disrupted the historical fire regime

The low-severity fire regime of the RMT has been disrupted. Stands that historically burned every 7–15 years last burned 48–140 years ago. As has been well-documented in dry fire-prone forests worldwide, multiple factors likely contributed to this change in the RMT, including climatic variation (Chavardès *et al.* 2019, 2020) and human impacts, as follows. The onset of the fire regime disruption coincides with changing land-use practices and introduction of fire management policies during settlement by Europeans. Reduced fire frequency in the late 19th century and early 20th century is commonly attributed to agriculture and grazing that reduced fine fuels and fire spread (Swetnam *et al.* 1999, Hessburg *et al.* 2019). More directly, the efficacy of fire prevention policies and suppression efforts are reflected in the virtual absence of surface fires since the 1940s and the BC Wildfire Service’s decades-long record of containing 94% of all surface wildfires (rank 1-4) by 10 am the day after discovery (BCWS 2021a).

While fire exclusion and suppression have successfully reduced fires, the prevention of Indigenous fire stewardship may have been a greater disruption of historical fire regime (Bowman *et al.* 2011; Lake and Christianson 2019). The RMT is within the traditional territory of the St. Mary’s (*?a’qam*) and Tobacco Plains (*?akinkum’lasnuqti?it*) bands of the Ktunaxa (ktunáx̣a) First Nation (Ktunaxa Nation 2021). Oral histories, settler ethnographies, and archaeological evidence highlight fire as an essential component of Ktunaxa culture and traditions (Smith 1984, Mah 2000, Munson 2006, Birdstone 2010). The Ktunaxa followed a

nomadic, seasonal subsistence pattern that included the hunting of deer, elk and bear in the RMT (Munson 2006), by encircling animals with fire to force them into desired areas (Smith 1984). Many of the plants and roots used for food, fiber, and medicine were cultivated in the grasslands and adjacent mountains of the study area (Mah 2000, Munson 2006), and depended on frequent fire to maintain their distribution and abundance (Mah 2000). Wild tobacco, a very important ceremonial plant, was cultivated by the Ktunaxa from seed (Smith 1984, pgs. 80, 202). Fire enhances the productivity of wild tobacco (Sadik 2014), and Indigenous cultivation practices consistently used fire in preparation for planting (Hammett 2000). A testament to Ktunaxa use of fire in tobacco cultivation may be the presence of hundreds of trees with multiple fire scars (range 15-52 scars tree⁻¹; this study and site VIZ from Heyerdahl *et al.* 2008) near the Tobacco Plains reserve (**Fig. 1.1**), named for the importance of the area for tobacco cultivation (Birdstone 2010, p. 4). Individual ponderosa pine trees with 52 (PPX02) and 32 (VIZ) scars attest to the prevalence of human-influences on the low-severity fire regime that dominated prior to the 20th century. Cultural use of fire would also explain the much higher fire frequencies in low-elevation valley bottoms relative to adjacent montane forests in the RMT in BC (Marcoux *et al.* 2013) and Montana (Barrett 1980, Barrett and Arno 1982, Gruell 1985, Heyerdahl *et al.* 2008). Concurrent with settlement by Europeans, Ktunaxa cultural fire practices were disrupted as they were displaced from their traditional territories to live on federal reserves (Lake and Christianson 2019) and colonial fire exclusion policies were enforced (Parminter 1981).

2.5 Conclusions

Contrary to the mixed-severity model, tree-ring reconstructions revealed a low-severity fire regime that once dominated the dry, mixed-conifer forests of southeastern BC. Although high-severity fires occurred, over 99.7% of fires were of lower severity. Given the intensive,

documented use of fire by the Ktunaxa, the low-severity fire regime was likely shaped by Ktunaxa fire stewardship. Rather than being products of past high-severity fires, contemporary dense stands are artefacts of forest management over the past 150 years. All contemporary subcanopy cohorts were initiated by moderate-severity fires, but additional fires, selective harvesting and climate interacted to facilitate high numbers of tree regeneration. Notable among disturbance sequences were harvesting and post-harvest fires that interacted to facilitate the greatest proportions of recruitment into dominant and co-dominant canopy positions. When interacting with suitable climate, these disturbances generated 44% of contemporary trees in a short 15-year period. In the absence of fire, dense stands persisted through time. Despite the effectiveness of contemporary fire suppression, the prevention of Ktunaxa fire stewardship may have disrupted the historical fire regime more than fire suppression. Fire exclusion and historical selective harvesting have interacted to generate nearly 80,000 ha of dense Douglas-fir, ponderosa pine and/or western larch forests with >400 live trees ≥ 12.5 cm dbh, or >800 live and dead trees >1.3 m height ha^{-1} , which comprise at least 56% of dry forests in the southern Rocky Mountain Trench of British Columbia, Canada. These dense stands represent degraded components of the dry forest matrix, and require extensive and immediate restoration to enhance their resilience to fire and climate change.

2.6 Tables

Table 2.1 Composition, structure and harvesting impacts on the 20 study stands in the Ponderosa Pine (PP) and Interior Douglas-fir (IDF) zones of the southern Rocky Mountain Trench.

Canopy trees were in the dominant and co-dominant height classes; subcanopy trees were in the intermediate and suppressed height classes. Tree species include Douglas-fir (PSME), ponderosa pine (PIPO) and western larch (LAOC). Stump decay classes were defined as follows: 1 = bark intact, wood hard, solidly in the ground; 2 = bark all or mostly intact, wood hard or soft, roots rotten, stump loose in ground; 3 = bark loose/sluffing, large portions of wood decayed; 4 = bark mostly sluffed, stump mostly or entirely debris.

Plot	Tree density (trees ha ⁻¹)				Tree relative composition (%)											
	Canopy	Subcanopy	Stumps		Canopy			Subcanopy			Stumps decay class 1-2			Stumps decay class 3-4		
			Decay class 1-2	Decay class 3-4	PSME	PIPO	LAOC	PSME	PIPO	LAOC	PSME	PIPO	LAOC	PSME	PIPO	LAOC
PPX02	85	1805	54	84	89	11	0	95	1	0	39	0	0	45	16	0
PPX03	126	4043	0	18	51	49	0	6	94	0	0	0	0	11	89	0
PPX04	162	3429	92	238	96	4	0	86	14	0	28	0	0	64	8	0
PPX07	201	3588	66	130	91	9	0	95	5	0	34	0	0	44	22	0
PPX08	173	2225	30	246	31	69	0	83	17	0	11	0	0	76	13	0
PPX09	590	5471	56	158	99	1	0	77	23	0	25	1	0	14	60	0
PPX10	183	2364	28	134	53	29	19	88	11	0	16	0	1	28	14	41
IDFX02	162	4078	10	58	80	18	2	94	4	0	15	0	0	35	0	47
IDFX03	185	21662	0	180	97	3	0	99	0	0	0	0	0	12	88	0
IDFX04	79	1019	2	152	31	42	20	48	43	6	1	0	0	56	4	39
IDFX05	177	4425	14	126	52	0	48	50	0	50	10	0	0	73	0	17
IDFX06	117	7008	6	44	75	0	25	91	0	6	0	0	12	48	0	40
IDFX07	281	2271	0	124	87	8	5	95	1	4	0	0	0	16	0	84
IDFX08	240	1281	0	162	92	0	8	71	0	29	0	0	0	58	0	42
IDFX09	112	2418	0	70	37	1	47	93	0	3	0	0	0	37	0	63
IDFX10	231	3925	0	70	1	0	99	21	0	77	0	0	0	11	0	89
IDFX11	312	3541	32	92	81	7	12	89	0	1	26	0	0	44	19	11
IDFX12	195	2178	0	118	94	5	1	97	3	0	0	0	0	69	8	22
IDFX13	157	1344	0	98	81	0	19	98	0	0	0	0	0	57	0	43
IDFX14	169	3612	14	44	92	1	8	50	0	49	24	0	0	21	7	48

Table 2.2 Disturbance history of the 20 study stands.

The number of fires reported are for the full fire recording period. Fire interval information (number of intervals, mean and range) is reported for the period when sample depth included ≥ 3 trees in each plot. Due to low stump sample depth in plot PPX03, the 1922 harvest date was derived from growth releases identified in surrounding trees.

Plot	Full fire record	Number of fires	Period of analysis	Fire Intervals			Time Since	
				n	mean (years)	range (years)	Last Fire (years)	Harvest (years)
PPX02	1388 - 2013	69	1401 - 2013	68	7.0	2-70	118	1917, 1959
PPX03	1192 - 2013	35	1547 - 2013	30	11.4	2-32	124	1922
PPX04	1337 - 2013	42	1525 - 2013	37	10.3	2-32	94	1912, 1962, 1976
PPX07	1496 - 2013	42	1506 - 2013	41	9.0	2-28	124	1907, 1927, 1955, 1963
PPX08	1422 - 2013	30	1482 - 2013	27	13.9	3-48	124	1912, 1960, 1969, 1994
PPX09	1481 - 1989	27	1731 - 1989	17	9.4	3-16	98	1915, 1966
PPX10	1456 - 2013	40	1541 - 2013	38	9.2	2-21	82	1917, 1951, 1980
IDFX02	1246 - 2013	31	1571 - 2013	20	14.0	3-34	140	1909, 1953, 1964, 1971
IDFX03	1166 - 2014	15	1803 - 2014	7	13.1	2-34	90	1922
IDFX04	1377 - 2013	38	1533 - 2013	32	11.6	2-45	82	1917, 1978
IDFX05	1397 - 2013	34	1694 - 2013	20	10.8	2-21	93	1907, 1939
IDFX06	1728 - 2013	16	1735 - 2013	15	14.0	3-37	48	1964
IDFX07	1461 - 2013	34	1739 - 2013	20	9.8	2-27	78	1937
IDFX08	1504 - 1914	24	1620 - 1914	23	12.6	2-51	104	1914
IDFX09	1844 - 2013	6	1847 - 2013	5	13.6	4-29	82	1942
IDFX10	1556 - 2013	29	1561 - 2013	28	13.1	2-50	67	1949
IDFX11	1601 - 2013	29	1613 - 2013	28	10.5	2-26	104	1919, 1959, 1968
IDFX12	1491 - 2014	37	1540 - 2014	33	11.6	2-34	87	1918, 1949
IDFX13	1585 - 2014	29	1667 - 2014	21	11.9	5-22	71	1922
IDFX14	1653 - 2014	16	1696 - 2014	14	14.9	5-33	108	1919, 1943, 1977, 1986

Table 2.3 Factors contributing to cohort initiation, facilitation, and persistence.

Cohort Init. is the year of cohort initiation; years in bold are the most recent cohorts in each plot. Initiating factors include the year and severity (moderate, high) of initiating fires, and harvest years that preceded cohort initiation. Facilitating factors include the years of fires, average Palmer Drought Severity Index (PDSI) value for the first 15 years following cohort initiation, and harvest years during facilitation periods. Highlighted PDSI values identify recent cohorts that were facilitated by wet/cool climate between 1896-1910. Year^{MAX} is the year the last tree established, and each stand reached its maximum contemporary density. Persistence includes years of harvest events that occurred in stands after they reached their contemporary densities. Year^{FE} is the year Time Since Last Fire exceeded the **longest reconstructed (i.e., maximum)** fire return interval.

Plot	Cohort Init.	Initiating factors (≤ cohort init.)			Facilitating factors (cohort init. to Year ^{MAX})			Year ^{MAX}	Persistence (> Year ^{MAX})	Year ^{FE}
		Fire	Severity	Harvest	Fire	Climate	Harvest		Harvest	
PPX02	1898	1895	Mod	-	No fires	1.03	1917, 1959	1974	-	1965
PPX03	1808	1804	Mod	-	-	-	-	-	-	-
	1893	1889	Mod	-	No fires	0.76	1922	1924	-	1921
PPX04	1882	1882	Mod	-	1893, 1901, 1910, 1919	-0.50	1912	1929	1962, 1976	1951
PPX07	1819	1815	Mod	-	-	-	-	-	-	-
	1882	1878	Mod	-	1887, 1889	-0.50	1907, 1927	1927	1955, 1963	1917
PPX08	1898	1889	Mod	-	No fires	1.03	1912	1923	1960, 1969, 1994	1937
PPX09	1885	1883	Mod	-	1889, 1905, 1908, 1915	-0.08	1915	1935	1966	1931
PPX10	1836	1834	Mod	-	-	-	-	-	-	-
	1884	1868	Mod	-	-	-	-	-	-	-
	1931	1931	Mod	1917	No fires	-0.92	-	1948	1951, 1980	1952
IDFX02	1868	1868	Mod	-	1873	0.27	-	1897	1909, 1953, 1964	1907
IDFX03	1892	1889	Mod	-	1923	0.54	1922	1928	-	1957
IDFX04	1915	1904	Mod	-	1920, 1931	-0.76	1917	1970	1978	1976
IDFX05	1904	1889	Mod	-	1908, 1920	0.70	1907, 1939	1955	-	1941
IDFX06	1863	1843	Mod	-	-	-	-	-	-	-
	1929	1919	Mod	-	1931, 1936	-1.03	-	1960	1964	2002
IDFX07	1806	1796	Mod	-	-	-	-	-	-	-
	1931	1931	Mod	-	1935	-0.92	1937	1964	-	1962
IDFX08	1906	1906	Mod	-	1909	0.39	1914	1929	-	1960
IDFX09	1838	No Record	High	-	-	-	-	-	-	-
	1931	1931	Mod	-	No fires	-0.92	1942	1981	-	1960
IDFX10	1763	1759	Mod	-	-	-	-	-	-	-
	1787	1779	Mod	-	-	-	-	-	-	-
	1931	1931	Mod	-	1946	-0.92	1949	1950	-	1996
IDFX11	1630	1629	Mod	-	-	-	-	-	-	-
	1750	1740	Mod	-	-	-	-	-	-	-
	1911	1909	Mod	-	No fires	-0.18	1919	1941	1959, 1968	1935
IDFX12	1761	1759	Mod	-	-	-	-	-	-	-
	1926	1926	Mod	1918	No fires	-1.26	1949	1953	-	1960
IDFX13	1920	1914	Mod	-	1936, 1942	-1.16	1922	1954	-	1964
IDFX14	1771	1765	Mod	-	-	-	-	-	-	-
	1905	1905	Mod	-	No fires	0.49	1919	1924	1943, 1977, 1986	1938

Table 2.4 Sequences of disturbances in each plot and the percent of canopy and subcanopy tree establishment during cohort facilitation periods.

The cohort facilitation period in each plot begins the year the most recent cohort initiated, and ends the year stands reached their contemporary densities. Disturbance sequences list the type (F = fire, H = harvest), number and order of disturbances. Tree establishment indicates the percent of canopy and subcanopy establishment in plots during facilitation periods. Canopy trees were in the dominant and co-dominant height classes; subcanopy trees were in the intermediate and suppressed height classes.

Plot	Facilitation period	Disturbance sequence	Tree Establishment (%)	
			Canopy	Subcanopy
PPX02	1898 - 1974	2H	85	92
PPX03	1893 - 1924	1H	74	100
PPX04	1882 - 1929	3F-1H-1F	94	93
PPX07	1882 - 1927	2F-2H	21	90
PPX08	1898 - 1923	1H	86	100
PPX09	1885 - 1935	3F-1H-1F	98	98
PPX10	1931 - 1948	No disturbances	1	87
IDFX02	1868 - 1897	1F	93	98
IDFX03	1892 - 1928	1H-1F	95	97
IDFX04	1915 - 1970	1H-2F	84	100
IDFX05	1904 - 1955	1H-2F-1H	90	100
IDFX06	1929 - 1960	2F	36	100
IDFX07	1931 - 1964	1F-1H	52	96
IDFX08	1906 - 1929	1F-1H	5	93
IDFX09	1931 - 1981	1H	33	99
IDFX10	1931 - 1950	1F-1H	0	87
IDFX11	1911 - 1941	1H	48	96
IDFX12	1926 - 1953	1H	42	98
IDFX13	1920 - 1954	1H-2F	61	95
IDFX14	1905 - 1924	1H	28	67

2.7 Figures

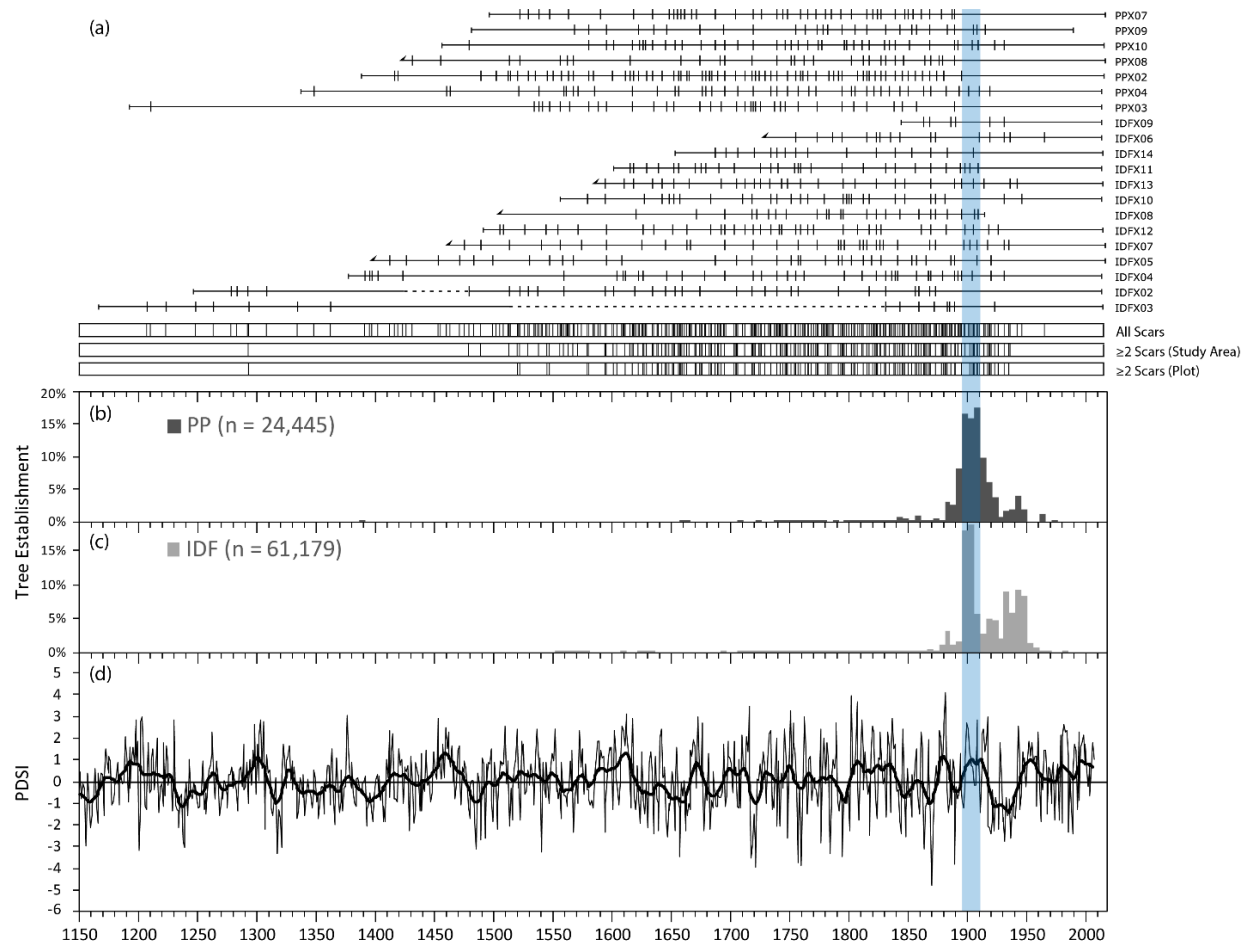


Figure 2.1 Chronologies of (a) fire occurrence, (b & c) tree establishment in the Ponderosa Pine (PP) and Interior Douglas-fir (IDF) biogeoclimatic zones, and (d) reconstructed Palmer Drought Severity Index (PDSI; Cook *et al.* 2008).

Fire chronologies are for each plot (horizontal lines), with summaries for all plots. For tree establishment, vertical bars indicate the proportion of contemporary trees that established per decade in the PP and IDF biogeoclimatic zones. The blue vertical bar indicates a 15-year period of wet, cool climate during which 44% of trees established.

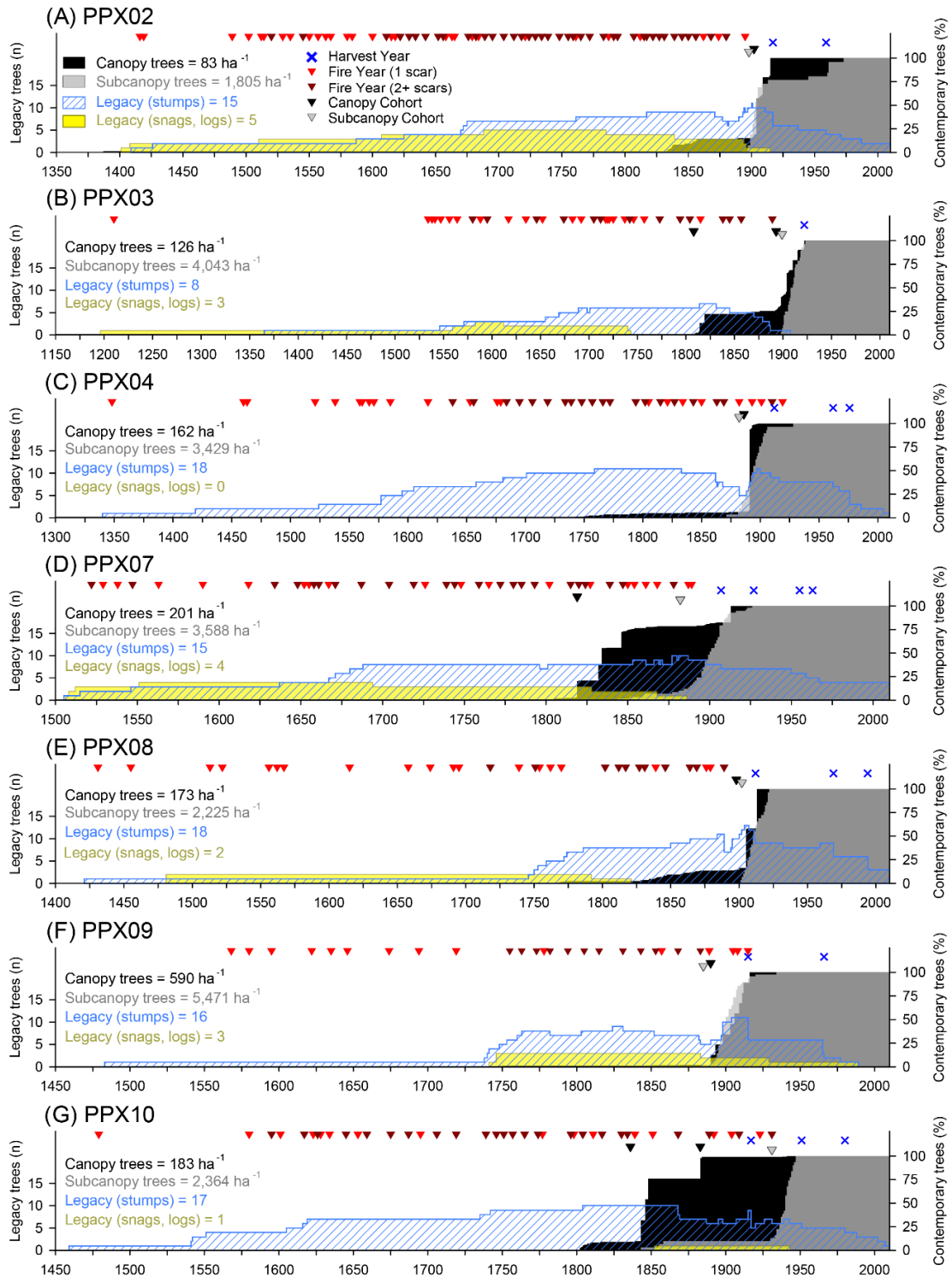


Figure 2.2 Stand demography, disturbance history, and sample depth (number per year) of legacy trees in seven plots representing dense stands in the Ponderosa Pine (PP) biogeoclimatic zone. Canopy trees were in the dominant and co-dominant height classes; subcanopy trees were in the intermediate and suppressed height classes.

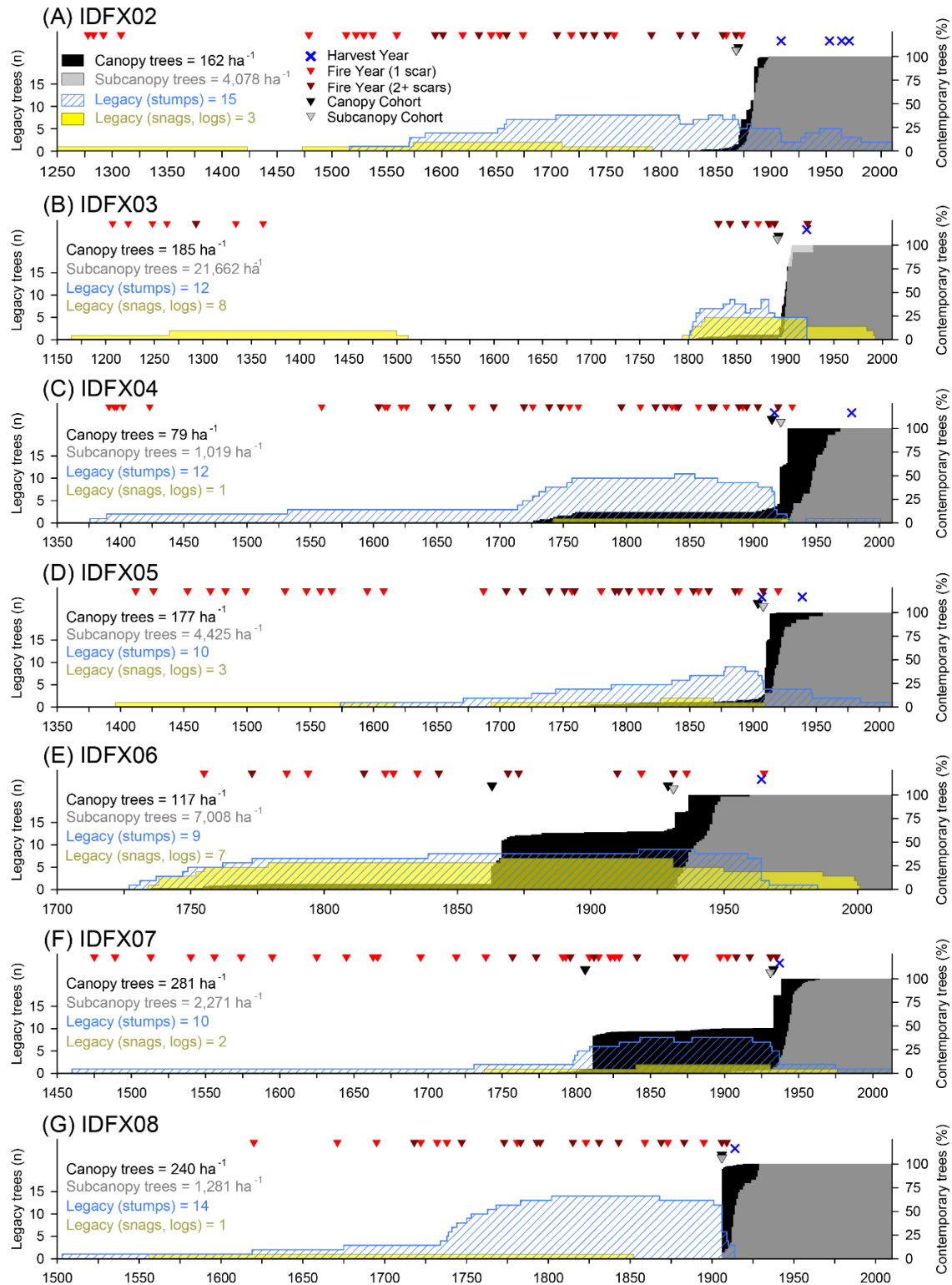


Figure 2.3a Stand demography, disturbance history, and sample depth (number per year) of legacy trees in seven plots (2-8) representing dense stands in the Interior Douglas-fir (IDF) biogeoclimatic zone. Canopy trees were in the dominant and co-dominant height classes; subcanopy trees were in the intermediate and suppressed height classes.

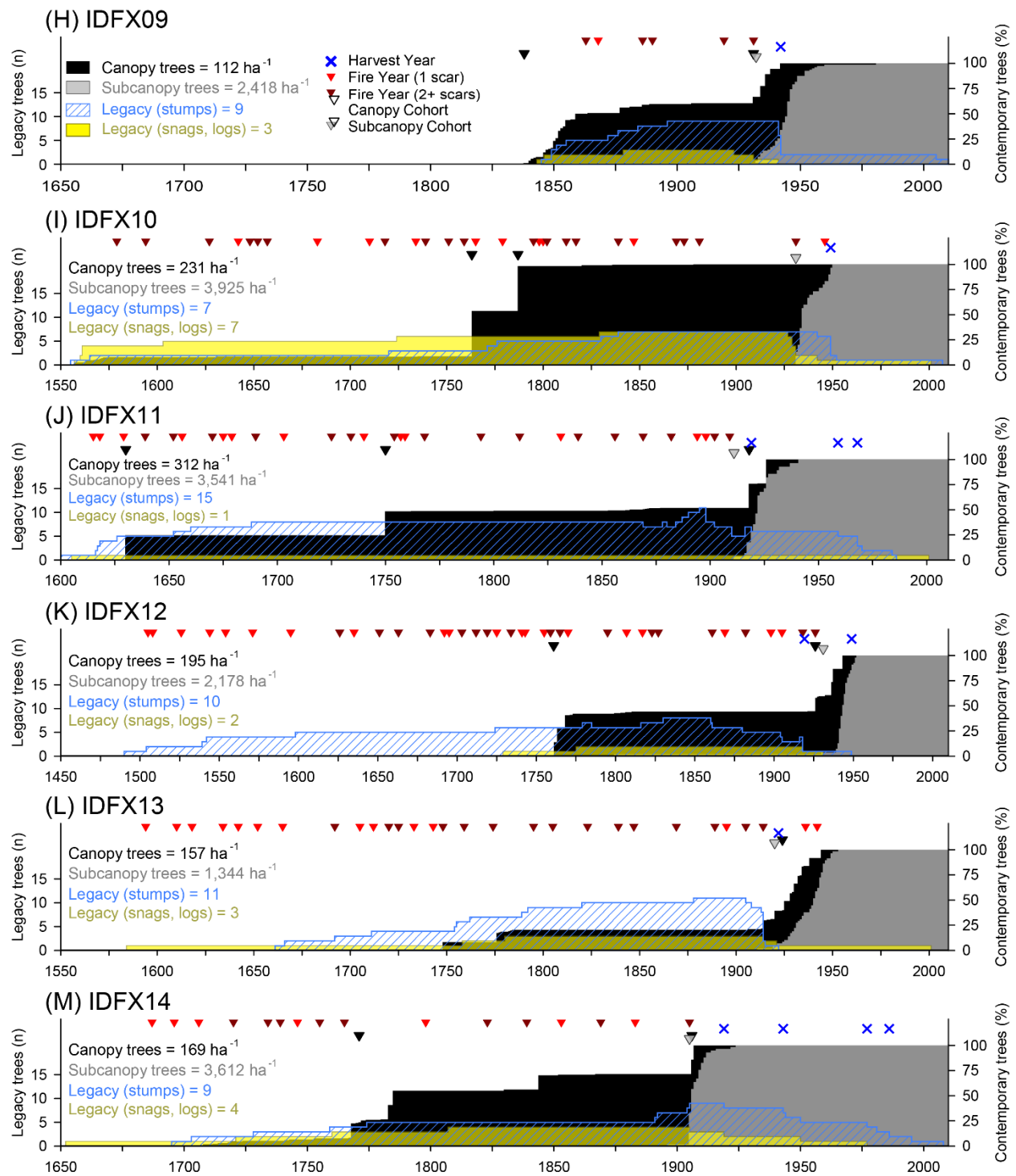


Figure 2.3b Stand demography, disturbance history, and sample depth (number per year) of legacy trees in six plots (9-14) representing dense stands in the Interior Douglas-fir (IDF) biogeoclimatic zone. Canopy trees were in the dominant and co-dominant height classes; subcanopy trees were in the intermediate and suppressed height classes.

Chapter 3: Harvesting and fire exclusion altered the resilience trajectories of dense dry forests in British Columbia

3.1 Introduction

The resilience of many fire-adapted forests in western North American forests have been degraded by a century of management focused on the exclusion of fire from forests (Stevens-Rumann *et al.* 2018, Hessburg *et al.* 2019). In dry mixed-conifer forests, fire exclusion has decreased the abundance of shade-intolerant species, favored establishment of shade-tolerant species, increased forest densities, and augmented the proportion of small trees relative to large trees (Fulé *et al.* 1997, Camp 1999, Knapp *et al.* 2013, Stephens *et al.* 2015, Collins *et al.* 2017). In addition, fire exclusion has enhanced susceptibility to crown fires and insect outbreaks, and amplified drought-stress through increased competition for water (Keane *et al.* 2002, Stephens *et al.* 2018, Hessburg *et al.* 2019, Voelker *et al.* 2019). Historical selective harvesting of large, fire-tolerant trees in the late 19th and early 20th century augments these effects (Naficy *et al.* 2010, Merschel *et al.* 2014). These changes are outpacing the ability of dry forests to reorganize and adapt to disturbances (Anderegg *et al.* 2019), causing shifts to alternate stable states (Harris and Taylor 2015, Chambers *et al.* 2016, Stevens-Rumann *et al.* 2018). Anticipated water deficits throughout the 21st century (Abatzoglou and Williams 2016, McKenzie and Littell 2017, Littell *et al.* 2018) will compound these effects, and further diminish the capacity of dry forests to recover after disturbances (Stevens-Rumann *et al.* 2018, Davis *et al.* 2019).

Ecosystem restoration can mitigate the negative effects of past management practices and enhance dry forest resilience to fire and other disturbances (Brown *et al.* 2005, Hessburg *et al.* 2015, Hood *et al.* 2016). To enhance resilience, most dry forest restoration treatments aim to thin

densely-stocked stands to open canopies, lower tree density, reduce the presence of small, shade-tolerant but fire-intolerant trees, and promote the growth of large, fire-tolerant trees (Hessburg *et al.* 2019). Historical stand structures and composition are often used as baselines to reconstruct the historical range of variability (HRV; Keane *et al.* 2009, Higgs *et al.* 2014) and guide thinning treatments (Swetnam *et al.* 1999). Numerous studies in the western United States (U.S.) have reconstructed historical stand density, basal area (BA), quadratic mean diameter (QMD), species composition, and trends in regeneration and mortality of contemporary dense, dry forests (Fulé *et al.* 1997, Sloan 1998, Camp 1999, Arno *et al.* 1999, Moore *et al.* 2004, Everett and Baumgartner 2007, Scholl and Taylor 2010, Knapp *et al.* 2013, Brown *et al.* 2015, Stephens *et al.* 2015, Collins *et al.* 2017, Battaglia *et al.* 2018).

Historical reconstructions of contemporary dense, dry forests in British Columbia, Canada, have not been accomplished, despite the implementation of ecosystem restoration projects since the late-1990s (Gayton and Hansen 1998, Bond *et al.* 2013). This lack of historical information is concerning given the intensive history of settlement and land-use throughout dry forests in the province. In British Columbia, dry forests containing various configurations of ponderosa pine (*Pinus ponderosa* Douglas ex Laws.), Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco var. *glauca* [Beissn.] Franco), and western larch (*Larix occidentalis* Nutt) are unique because they grow in the bottoms of warm, deep valleys. Consequently, these forests overlap with areas that were intensively inhabited by Indigenous people and European settlers, and intensively harvested throughout the 19th and 20th centuries (Chapter 2). As such, human effects on stand development throughout the 20th century were likely profound, and have large implications for ecosystem restoration treatments in these areas. Given the lack of research, it remains unclear (i) if historical stand composition, structure and configurations have been

altered, as is well documented in dry forests of the western U.S., (ii) how fire exclusion and historical harvesting have shaped stand development, (iii) if dense stands represent degraded components of the dry forest matrix, or (iv) what the trajectory of these stands would be if there is no restoration in the future. Consequently, it is unknown if ecosystem restoration is warranted, or if past and present treatments are promoting configurations that are within the historical range of variability.

The goal of this study is to reconstruct the historical composition and structure of British Columbia's dense, dry mixed-conifer forests to address these knowledge gaps. To accomplish this goal, I examined how the interactive effects of fire exclusion and historical harvesting shaped stand composition, structure and development, and altered the regeneration and mortality dynamics of dense, dry forests through time. I asked three primary questions: (1) How did fire exclusion, historical harvesting and their interactions shape stand development? (2) Are contemporary stand configurations within the historical range of variability? (3) In absence of ecosystem restoration, do current trends in regeneration and mortality indicate resilience of contemporary stands to fire and other disturbances? In this context, resilience is defined as the ability of forests to absorb or withstand disturbances, then recover and reorganize without shifting to a different state (Holling 1973, Holling 1996, Resilience Alliance 2021). To answer these questions, I used survey data and tree-rings to reconstruct fire history, harvest history, and changes in species composition, density, BA, QMD, regeneration and mortality through time. Understanding the drivers and trajectories of change in dry forests is critical for designing science-based fuels mitigation and ecological restoration treatments that enhance forest resilience to fire and other disturbances.

3.2 Methods

3.2.1 Study area and research design

This study was conducted in the southern Rocky Mountain Trench (RMT) located in southeastern British Columbia, Canada (Chapter 1). The research design was described in Chapter 2.

3.2.2 Harvest and fire history

To reconstruct harvest history, I documented stumps in half of each 1-ha plot. I recorded the species, decay class (1-4; Chapter 2), stump height and inside-bark diameter, and whether stumps continued growing post-harvest (i.e., were “living stumps”), as evidenced by the presence of regenerative tissues growing over or near the top of stumps (Bormann 1966). Attempts to determine the species of each stump were made using remnant bark, and the decay status, color, and odor of remaining wood. I recorded stump height and inside-bark diameter to reconstruct pre-harvest DBH using species-specific equations (Omule and Kozak 1989). To determine the years of harvest, I sampled up to 10 stumps per plot with intact bark and/or phloem present. I aimed to sample a minimum of 3 stumps from each of decay classes 1-2 and decay classes 3-4 that were nearest to plot center, to test the hypothesis that classes 1-2 represented more recent harvests and classes 3-4 represented older harvests. Living stumps were prioritized, as they yielded the soundest wood to reconstruct harvest dates.

I reconstructed the fire history of each stand to determine (a) when the last fire occurred, and (b) the mean and maximum (i.e., longest reconstructed) plot-level fire return intervals (Chapter 2). Within each 1-ha density plot I identified all fire-scarred trees, snags, stumps, and logs. Fire-scar samples were removed with a chainsaw from at least 10 live and dead trees that

had the greatest number of visible, well-preserved scars. To reduce impacts on live trees and snags, I removed partial cross-sections (Arno and Sneek 1977) whenever it was safe to do so, using WorkSafe BC sanctioned protocols (Cochrane and Daniels 2008). I bolstered the fire scar sample size by including the samples from stumps that had fire scars.

3.2.3 Stand structure and composition

To represent the contemporary stand and reconstruct historical structure and composition, I censused all canopy-dominant trees, those with crown tops extending ≥ 1 m above the general canopy, in each 1-ha plot and recorded species, diameter at breast height (DBH), and condition. Smaller trees were sampled in subplots centered on 1–3 randomly selected canopy-dominant trees of differing species per plot; more subplots were placed in stands with multiple species of canopy-dominant trees. An 11.28 m-radius plot (0.04 ha) was placed around selected canopy-dominant trees; in one stand with density $>18,000$ trees ha^{-1} , an 8m-radius plot (0.02 ha) was used. For each tree I recorded species, condition and DBH. To determine establishment dates, and reconstruct mortality and basal area through time, I extracted increment cores or cross-sectional disks from all live and dead canopy-dominant trees in the 1-ha plot, and the 10 nearest trees (live and dead) in each of four DBH classes (dominant: ≥ 30 cm, mature: 12.5–29.9 cm, pole: 7.5–12.49 cm, sapling: <7.5 cm and >1.3 m height) in each subplot, up to the subplot radius. Canopy-dominant trees with excessive wood decay were documented but not sampled. In subplots, decayed trees were replaced with the next nearest tree in the same size class. For each sampled tree with DBH ≥ 12.5 cm, I obtained two opposing cores from within 30 cm of the ground. Multiple cores were extracted from each side to ensure rings were within an estimated 10 rings of pith. For sampled trees <12.5 cm DBH, full cross-sections were cut within 5 cm of the ground. Sample height and diameter at sample height were recorded for all sampled trees,

and distance from plot center was recorded for all trees sampled in subplots.

In each 1-ha plot, I also documented the presence of live and dead trees that were likely components of historical stand structures (hereafter “legacy trees”). These included trees that were (a) not canopy-dominant, and (b) unrepresented in sample plots, but met at least one of the following criteria: (i) a live tree or snag with a broken top that would have been included as a canopy-dominant in the contemporary canopy strata had the top been attached; or (ii) a living or remnant tree (log or snag) that had charred bark or a fire scar. For each tree, I recorded species, condition and DBH.

To determine contemporary regeneration density (trees ≤ 1.3 m height) by species, I sampled three points at the center, northern and southern edges of each 1-ha plot. The species and condition (i.e., live or dead) of all regeneration were tallied within 5.64 m (0.01 ha) of each point, and values from the three points were averaged for each plot.

3.2.4 Dendrochronological reconstructions of disturbances and forest structures

Samples were air dried, mounted to wooden supports as needed (e.g., cores and unstable cross-sections), sanded with progressively finer sandpaper to 600 grit, and scanned at the highest resolution possible for the size of the sample (1200, 2400, 3200 or 4800 dpi). The ring widths of all scanned images were measured (to 0.001mm) and cross-dated using the computer programs CooRecorder and CDendro (v9.0, Cybis Elektronik 2018). All samples were cross-dated to determine the calendar years of the outer- and inner-most rings, and the year and season of each fire for fire-scar samples (Dieterich and Swetnam 1984). Outer-ring dates on stumps indicated the year of harvest. Since lightning ignitions in the study area occur primarily in the summer or fall, I assigned fire scars along ring boundaries (i.e., dormant season scars) to the earlier of the two adjacent calendar years.

Plot-level fire intervals were computed by compositing fire dates from all fire-scarred samples in each plot into a single record (Dieterich 1980). Samples from harvested stumps that had fire scars were included. Mean and maximum plot-level fire return intervals were calculated with the program *Fire History Analysis and Exploration System* (FHAES 2.0.2; Brewer *et al.* 2016), using fire interval distributions that included all fire scars (e.g., all fires that scarred ≥ 1 tree). However, fire frequency statistics were only calculated for the period beginning when sample depth included ≥ 3 trees per plot, to minimize the effects of older fire scars having been removed by subsequent fires. I calculated the time since the last fire (TSLF) for each plot as the number of years from the last fire to the year 2013.

Years of establishment for sampled trees were calculated from cross-dated pith or inner-ring dates. A geometric correction was applied to estimate the number of missing rings for the subset of increment cores that did not intercept the pith (Duncan 1989). For all increment cores and disks, the number of years for trees to grow to sample height was determined using species-specific regressions (Villalba and Veblen 1997, Wong and Lertzman 2001). Regressions were developed from 35, 28, 12 and 18 regenerating Douglas-fir, ponderosa pine, western larch and lodgepole pine samples, respectively, that were 20–150 cm in height and grew in open conditions in 10 study plots. Individuals were uprooted or cut at the root-shoot interface and sectioned at 10 cm intervals. The 10 cm sections were sanded to 600 grit and ring counts were used to develop species-specific regressions of age (ring counts) on height that were applied to estimate the number of years to grow to sample height ($r^2 = 0.89\text{--}0.93$, SEE = 2.81–7.78 years; **Appendix A**). The year of establishment for each sampled tree was calculated as the inner-ring date minus the corrections for missed rings and sample height (Daniels *et al.* 2017). For harvested stumps, since I was only concerned with determining harvest years, I did not correct

inner-ring dates of harvest samples by the number of missed rings to the pith, nor for the number of years for each tree to grow to sample height.

Linear regression models comparing age-DBH relationships of sampled trees were used to estimate establishment years and ages of 84 unsampled canopy-dominant and legacy trees (**Appendices B and C**). Models were developed for each plot, with DBH, DBH size class, species and condition as explanatory variables ($\alpha=0.05$; SAS GLM Procedure, SAS Institute 2018). On average, age-DBH relationships explained 74% of the variation in establishment data, and 78% of the variation in age data. Outer ring dates of live trees were assigned the year 2013. For dead trees, outer ring dates were assigned as the modeled establishment year plus the estimated age of the tree. I modeled establishment year but not death year because trees with similar DBH tended to establish closer together in time (e.g., in small post-disturbance pulses; Chapter 2); relationships between years of death and tree size were less apparent.

To quantify growth trends, ring-width series from sampled trees were converted to basal area increment (BAI) using the following equation:

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where r_t corresponds to the outer-bark tree radius at DBH at the end of year t, and r_{t-1} corresponds to the outer-bark tree radius at DBH at the end of year t-1. Since all samples were taken near ground level, I used species-specific allometric equations to model DBH (Omule and Kozak 1989) from inside-bark diameter at sample height for each calendar year. Prior to converting to BAI, DBH values were rescaled to ensure the outermost diameter matched the DBH measured at the time of sampling.

3.2.5 Defining harvesting periods

The species and DBH of all surveyed stumps in decay classes 1-2 and 3-4 were

summarized for each plot. I grouped the subset of stumps with harvest dates by decay class to test the hypothesis that decay classes 1-2 represented recent harvests, whereas classes 3-4 represented older harvests. Since the harvest dates were non-normally distributed, I compared medians using Mann-Whitney U Tests ($\alpha = 0.05$; SigmaPlot v11.0, SYSTAT 2008) and determined 1951 was the intermediate harvest date between the two decay groups. The year 1951 was used to distinguish stumps harvested in Period 1 (≤ 1951) from those harvested in Period 2 (> 1951). For each plot, the first harvest year in Periods 1 and 2 were determined and used as a reference date for reconstructions in subsequent analyses.

3.2.6 Inferring fire exclusion

Fire exclusion was considered effective in each plot if time since last fire (TSLF) exceeded the maximum plot-level fire return interval. For each stand reconstruction period, I used the mean plot-level fire return interval to estimate the number of missed fires from the year of the last fire until the reference year, had fires continued burning at historical return intervals.

3.2.7 Temporal changes in stand structure, composition, regeneration, and mortality

Contemporary stand composition and structure (i.e., density, DBH and BA) represented conditions in the year 2013. Historical structure and composition of each plot were reconstructed for Period 1 and Period 2 reference years. Species composition and density were reconstructed for all trees (height > 1.3 m) and regeneration (height ≤ 1.3 m), whereas DBH and BA were only reconstructed for trees (height > 1.3 m). Establishment dates were used to identify live trees in each reference year. For all live trees, DBH and BA were reconstructed using different approaches for sampled and unsampled trees. For sampled trees, species-specific regressions of age on height (**Appendix A**) were used to determine which trees had at least one ring present at breast height (1.3 m); this distinguished regeneration (0 rings present) from trees (≥ 1 ring

present). For all trees, I reconstructed the diameter inside the bark at sample height and used species-specific allometric equations to model DBH (Omule and Kozak 1989) and calculate BA. For 84 unsampled canopy-dominant and legacy trees, species-specific linear regressions were used to reconstruct DBH in Period 1 and Period 2 reference years (**Appendices D and E**). Models were developed for each plot, with DBH, tree age, species, and condition as explanatory variables ($\alpha=0.05$; SAS GLM Procedure, SAS Institute 2018). On average, regressions explained 79% of the variation in Period 1 DBH data, and 97% of the variation in Period 2 DBH data. Modeled DBH values were used to calculate BA for unsampled trees in reference years.

To determine if stand structures changed significantly over time, I used paired t-tests ($\alpha = 0.05$; SigmaPlot v11.0, SYSTAT 2008) to compare the Period 1 reconstruction against the Period 2 reconstruction, and the Period 1 and Period 2 reconstructions against Contemporary conditions. The stand structure parameters assessed were mean density (number of trees per 1-ha plot), basal area (BA; m² per (i) 1-ha plot and (ii) DBH size class), and quadratic mean diameter (QMD; cm per 1-ha plot) for trees >1.3 m height. Density and BA were calculated as:

$$\text{Density} = \sum_i^n k_i \quad (2)$$

$$\text{BA} = \sum_i^n \left[k_i * \pi * \left(\frac{\text{DBH}_i}{200} \right)^2 \right] \quad (3)$$

where i represents the i th sampled tree in plots, n is the total number of sampled trees in plots, k is a scaling factor to convert individual trees to 1-ha equivalents, and DBH is diameter at breast height of each tree in cm. The scaling factor k was equal to 1 for canopy-dominant and legacy trees and 2 for trees reconstructed from stumps, but varied for trees in subplots, depending on the distance of the furthest sampled tree in each DBH size class from plot center. BA was summarized for each 1-ha plot, and for each DBH size class within plots. QMD was calculated as:

$$QMD = \sqrt{\frac{BA}{0.0000785 * Density}} \quad (4)$$

where BA is m² of basal area ha⁻¹, and Density is the number of trees ha⁻¹. T-tests were conducted on raw data unless log(x+1) transformations were needed to meet the assumption of normality. Data for Period 1 and Contemporary tree densities, and Period 1 and Contemporary sapling BA were not normally distributed, so a Wilcoxin Signed-Rank Test was used instead. Raw data are reported in all tables and figures.

3.2.8 Assessing departures from the Historical Range of Variability

To determine if contemporary dense stand configurations are within the historical range of variability (hereafter “HRV”), I derived baseline metrics from all pre-harvest stand reconstructions. Baseline metrics included total stand density, BA, and QMD, and the density and BA of each species in each stand. Three separate baselines were constructed based on species assemblage to ensure equitable representation of historical conditions, one for stands comprised of ponderosa pine and Douglas-fir, one for stands comprised of western larch and Douglas-fir, and one for stands with all three species. Baseline values were compared against the same metrics from contemporary stands to determine if contemporary values were within the range (minimum to maximum) of baseline values. A point was awarded to stands for each contemporary metric that was within the range of baseline values. Stands were classified into one of three HRV categories based on the percentage of points earned, as follows: (1) stands that scored 100% were “Within” the HRV, (2) stands with a score of 0% were “Outside” the HRV, and (3) all other stands were “Transitional.” The degree of departure from the HRV was calculated for each stand based on the percentage of points earned: High (0-33%), Moderate (34-66%) and Low (67-100%). To compare trends among species assemblage groups, the average degree of departure was calculated from stands in each group.

3.3 Results

3.3.1 Harvest and fire histories

I censused 1,374 stumps among the 20 plots (**Table 3.1**). Plots averaged 137 stumps ha⁻¹ (range 18-330); more stumps were in PP ($\mu = 191 \pm 101$) than IDF ($\mu = 109 \pm 43$) plots. Stumps were primarily Douglas-fir (73% in PP, 48% in IDF), with numerous ponderosa pine (22% in PP, 14% in IDF) and western larch (5% in PP, 37% in IDF). Most stumps were in decay classes 3 (67%) and 4 (18%). PP plots had more stumps in decay classes 1 and 2 (10% and 14%, respectively) than IDF plots (3% and 2%, respectively). Nearly all ponderosa pine and western larch stumps (99%) were in decay classes 3 and 4, compared with only 76% of Douglas-fir stumps. Most stumps were from larger diameter trees (76% ≥ 12.5 cm DBH, 57% ≥ 30 cm DBH), although PP plots had more small trees harvested (40% < 12.5 cm DBH) than IDF plots (9% < 12.5 cm DBH). A total of 194 living stumps were identified in 15 plots; most were from small trees (73% < 12.5 cm DBH).

To derive harvest dates from outer ring dates, 157 stumps were sampled, averaging 8 samples per plot (range 2-12; **Table 3.1**). Due to advanced decay, only 2 and 4 stumps were sampled in plots PPX03 and IDFX12, respectively; harvest dates were corroborated by radial growth releases in PPX03. Harvest dates differed significantly (Mann-Whitney U-test = 400.5, $P < 0.001$) by decay class. The median harvest date for stumps in decay classes 3-4 was 1917 (25th-75th percentile = 1914-1942), and was 1965 (25th-75th percentile = 1959-1976) for stumps in decay classes 1-2.

A total of 42 harvest events (43% in PP plots, 57% in IDF plots) and 32 unique harvest years were derived from outer ring dates and supplementary lines of evidence. All reconstructed

harvesting took place from 1907-1994, with most harvesting (55%) prior to 1951. Multiple harvest years (range 2-4) were identified in 12 plots; the first harvest occurred on or before 1919 in these plots. All PP plots were harvested at least once by 1922, and all but one of the IDF plots were harvested at least once by 1949. In IDFX06, a single harvest occurred in 1964.

Of 248 fire-scarred trees ($\mu = 12$ per plot, range 10–17) that I sampled, most were from western larch and ponderosa pine (44% and 46%, respectively), and the remainder were from Douglas-fir (10%). I dated 1,646 fire scars between 1207 and 1965, with an average of seven scars per sample (range 1–52). The last fire scar in each plot formed between 1873-1965 (**Table 3.2**). Prior to the last fire, plot-level fire return intervals averaged 11.6 years for all scarred trees (range 7.0-14.9 years) during the period beginning when sample depth included at least three trees. Maximum fire return intervals averaged 35 years (range 16-70), while the time since the last fire averaged 96 years (range 48-140).

3.3.2 Stand structure and composition

A total of 1,555 trees (14% dead) were used to reconstruct contemporary and historical stand structure and composition. The contemporary density of live trees (height >1.3 m, hereafter “live trees”) averaged 2,730 (range 874-14,219) ha^{-1} (**Table 3.3, Figs. 3.1-3.2**). Mean BA and QMD were 30.3 $\text{m}^2 \text{ha}^{-1}$ (range 18.5-41.2) and 13.9 cm (range 5.8-20), respectively. Stand densities and BA were dominated by Douglas-fir (81% and 76%, respectively) (**Figs. 3.1-3.2, Appendix F**). Ponderosa pine and western larch comprised 10% and 8% of stand densities, and 14% and 10% of stand BA, respectively.

The year of the first harvest occurred prior to 1951 (i.e. in Period 1) in 19 of the 20 study plots (**Table 3.3, Figs. 3.1-3.2**). The reconstructed density of live trees prior to harvesting averaged 184 ha^{-1} (range 76-354). Mean BA and QMD were 20.2 $\text{m}^2 \text{ha}^{-1}$ (range 6.4-31) and 37.6

cm (range 28.4-49), respectively. Species abundance was much more evenly distributed than in contemporary stands (**Figs. 3.1-3.2, Appendix F**). Individually, density and BA were dominated by Douglas-fir (52% and 39%, respectively), whereas ponderosa pine and western larch comprised nearly equivalent density (25% and 23%, respectively) and BA (31% and 30%, respectively). Collectively, ponderosa pine and western larch dominated BA across the study area (61%) and were nearly as abundant as Douglas-fir (48%). Ponderosa pine comprised the most BA in PP plots (60%), and western larch and Douglas-fir comprised similar BA in IDF plots (44% and 43%, respectively).

Eleven plots were harvested in Period 2 (i.e., after 1951), ten of which were first harvested in Period 1. Prior to Period 2 harvesting, the density of live trees averaged 2,228 ha⁻¹ (range 270-6,643) (**Table 3.3, Figs. 3.1-3.2**). Mean BA and QMD for all plots were 13.3 m² ha⁻¹ (range 8.3-20.1) and 12 cm (range 4.2-23.4), respectively. Live tree composition in all but two plots were dominated by Douglas-fir (71%) (**Figs. 3.1-3.2, Appendix F**). Similarly, BA was dominated by Douglas-fir (65%) across plots, with 66% and 64% of BA in PP and IDF plots, respectively. Ponderosa pine occupied nearly as much BA as in Period 1 (26%), but western larch comprised much less BA (8%).

3.3.3 Regeneration and mortality

In contemporary stands, the density of live regeneration (height ≤ 1.3 m, hereafter “regeneration”) averaged 675 ha⁻¹ (range 0-5,034) for all plots, though regeneration was absent in 50% of plots, and had fewer than 70 trees in 20% of plots. Regeneration densities were dominated by Douglas-fir (99%). Ponderosa pine represented 3% of regeneration in IDFX04 and Rocky Mountain juniper represented 3% of regeneration in PPX02, but both species comprised < 1% of overall regeneration. Western larch regeneration was absent from contemporary stands.

In Period 1, the density of live regeneration averaged 2,461 (range 0-18,826) but was absent in two plots and had 83 or fewer individuals in three other plots. Plots with few or no regeneration had subsequent fires recorded after Period 1 reconstruction years, whereas all plots with the last fire occurring prior to reconstructions contained 320 or more regenerating individuals. In plots with regeneration, densities were dominated by Douglas-fir (70%), followed by western larch (16%) and ponderosa pine (14%) (**Figs. 3.1-3.2**).

In Period 2, the density of live regeneration averaged 1,136 (range 0-6,335) across all Period 2 plots (**Table 3.3, Figs. 3.1-3.2**); regeneration was absent in three of these plots and contained 73 or fewer individuals in three other plots, but no subsequent fires were recorded. When regeneration was present, plot densities were dominated by Douglas-fir (80%), though Rocky Mountain juniper (13%), ponderosa pine (7%) and western larch (1%) were present.

All contemporary plots had dead trees (height >1.3 m, hereafter “dead trees”). The average density of dead trees across plots was 978 (range 1-4,720), and comprised an average BA of 1.9 m² (range 0.1-5.7) (**Table 3.3**). IDF plots had a higher average density of dead trees (n = 1,173) compared with PP plots (n = 617). Most dead trees were saplings (77%), followed by pole (12%), mature (6%) and dominant (5%) trees (**Fig. 3.3**). Dead trees were predominantly Douglas-fir (72%), followed by ponderosa pine (18%) and western larch (10%). Dead trees comprised 24% (range 0-54%) of average total (live and dead) stand densities, and 6% (range 1-19%) of average total stand BA. When considering the proportion of dead trees to all trees in each DBH size class, an average of 44% (range 0-100%) of saplings in stands were dead, 12% (range 0-60%) of poles were dead, 3% (range 0-22%) of mature trees were dead, and 6% (range 0-57%) of dominant trees were dead (**Fig. 3.3**). IDFX08, which had the lowest density of live trees (n = 401), had the greatest proportions of dead saplings (95%), poles (100%) and mature

(19%) sized trees. All dominant sized trees were dead in IDFX06.

Far fewer trees were dead in plots in Periods 1 ($n = 3$) and 2 ($n = 855$) than in contemporary stands ($n = 19,569$), but there were many more dead trees in Period 2 than in Period 1. Dead trees in Period 1 comprised 0.5 m^2 of BA; one tree was ponderosa pine, two were western larch, and all were $\geq 30 \text{ cm}$ DBH. An average of 78 trees ha^{-1} (range 0-492) were dead across plots in Period 2, and comprised an average of 0.1 m^2 of BA per plot. Nearly all dead trees were Douglas-fir saplings (94%) and ponderosa pine poles (5.8%).

3.3.4 Reconstructed harvesting

Harvesting in Period 1 removed an average of 66% of trees (range 24-100%) and 88% of BA (range 57-100%) (**Table 3.3, Figs. 3.1-3.2**). However, harvesting removed greater portions of BA from PP plots (90%) than IDF plots (86%). Trees of all sizes were removed, but harvesting in Period 1 targeted the largest trees, with an average of 91% (range 65-100%) of trees with DBH $> 30 \text{ cm}$ removed (**Figs. 3.1-3.2**). Period 1 harvesting clearly favored western larch; an average of 78% (range 37-100%) of its density and 94% (range 82-100%) of its BA were removed. Harvesting in Period 1 also favored large ponderosa pine over Douglas-fir; harvesting removed equivalent proportions of ponderosa pine and Douglas-fir densities (63% and 65%, respectively), but 89% of ponderosa pine BA was removed, whereas 78% of Douglas-fir BA was removed.

Period 2 harvesting removed an average of 4% of trees (range 0.2-19%) and 9% of BA (range 0.3-59%) (**Table 3.3, Figs. 3.1-3.2**); however, these values were skewed by the first and only harvest in plot IDFX06, which removed 19% of trees and 59% of BA. In this plot, harvesting removed 72% of trees with DBH $> 30 \text{ cm}$ and appears to have targeted Douglas-fir, with 53% ($n = 24$) of its density and 77% of its BA removed. Western larch was also harvested,

but only 12% ($n = 26$) of its density and 42% of its BA were removed. In all other plots, Period 2 harvesting represented the second or greater harvest, and removed an average of 2% of trees (range 0.2-6%) and 5% of BA (range 0.3-14%). In these multiple-entry plots, large trees were cut when they were present, but trees <12.5 cm DBH were targeted (64% of harvested trees), particularly pole-sized trees (47% of harvested trees). Douglas-fir was selected over other species, with 2% ($n = 380$) of its density and 4% of its BA within stands removed. Only two western larch and two ponderosa pine trees were harvested.

3.3.5 Inferred fire exclusion

Time since last fire exceeded maximum fire return intervals in all plots, indicating fires in the study area were successfully excluded for 48 to 140 years. Fire exclusion affected 58% of plots with harvesting in Period 1; an average of 1.4 fires (range 0.2-3.1) were missing at reference years (**Table 3.2**). Fire exclusion affected 91% of plots with harvesting in Period 2; an average of 5.7 fires (range 4.1-9.1) were missing at reference years. All plots were missing an average of 8.6 fires (range 3.4-16.9) by the year 2013.

3.3.6 Stand changes through time

For live trees, contemporary density (Z -test = 3.803) and BA (t -test = -3.967) were significantly greater, and QMD (t -test = 14.353) was significantly smaller than in Period 1 ($P < 0.001$ for all; **Table 3.4**). Only contemporary BA was significantly greater than Period 2 (t -test = -5.883, $P < 0.001$). The contemporary average density of trees increased 1463% over Period 1 densities. Contemporary BA averages were 148% larger and QMD averages were 63% smaller than Period 1 values. Shifts in contemporary BA from Period 1 values were significant for all DBH classes (Z -test_{Sapling} = 3.724, t -test_{Pole} = -11.514, t -test_{Mature} = -11.259, t -test_{Dominant} = 4.626, $P < 0.001$ for all; **Table 3.4, Fig. 3.4**), with a 7406% increase in the BA of saplings, a 2199%

increase in poles, a 712% increase in mature trees, but a 55% reduction in dominant trees. The contemporary average BA was 218% larger than BA in Period 2. Shifts in contemporary BA from Period 2 values were significant for the pole (t-test = -2.273, $P = 0.037$) and mature (t-test = -4.864, $P < 0.001$) tree size classes, with a 179% increase in the BA of poles and a 426% increase in mature trees. The contemporary average BA of saplings was 4% smaller than Period 2 values, and contemporary average BA of dominant trees were 164% larger, but differences were not significant ($P = 0.927$ and $P = 0.150$, respectively).

For the 10 plots with harvesting in both Periods 1 and 2, the density, BA and QMD of live trees differed significantly ($P = 0.008$, 0.045 and < 0.001 , respectively; **Table 3.4**). Average tree density in Period 2 represented a 1115% increase over Period 1 densities, but BA and QMD averages were 33% and 68% smaller, respectively. Shifts in BA in sapling, pole and dominant tree size classes were significant (t-test = -3.465 and $P = 0.007$, t-test = -5.27 and $P < 0.001$, t-test = 5.87 and $P < 0.001$, respectively; **Table 3.4, Fig. 3.4**), with a 3797% increase in the BA of saplings, an 868% increase in poles, but a 79% reduction in dominant trees. The BA of mature trees in Period 2 increased 134% from Period 1 values, but was not significant ($P = 0.173$).

3.3.7 Departures from the Historical Range of Variability (HRV)

Pre-harvest metrics from all plots in Period 1, and plot IDFX06 in Period 2 were used to reconstruct baselines for the HRV (**Appendices G-L**). Three separate baselines were created from seven stands with species assemblages comprised of ponderosa pine and Douglas-fir (hereafter “PIPO-PSME”), five stands comprised of western larch and Douglas-fir (hereafter “LAOC-PSME”), and eight stands comprised of all three species (hereafter “LAOC-PIPO-PSME”)(**Table 3.5, Fig. 3.5**). No stands were within the HRV. One PIPO-PSME stand was outside the HRV, while all other stands were transitional. Among species assemblage groups, the

maximum average score was 32%, indicating all groups exhibited a high degree of departure from the HRV. Stands in the LAOC-PIPO-PSME group had the highest scores (group average 32%, range 22-56%), with four stands having a moderate-degree of departure. Similarly, two stands in the LAOC-PSME group had a moderate-degree of departure, but stand-level scores were lower (group average 31%, range 14-43%). The PIPO-PSME group was the most departed from the HRV, with an average score of 20% (range 0-43%). Ponderosa pine density and basal area were within the HRV in 75% of stands in the LAOC-PIPO-PSME group, and western larch density and basal area were within the HRV in 40% of stands in the LAOC-PSME group.

3.4 Discussion

Stand reconstructions revealed much about the history, drivers of change, and future trajectories of dense, dry mixed-conifer forests in southeastern B.C. First, historical stands were much less dense, had open canopies, and a high proportion of large, fire-tolerant trees relative to contemporary stands. All contemporary stands have become dense, containing hundreds to thousands of small, fire-intolerant but shade-tolerant Douglas-fir trees. The abundance of smaller trees contributed to stands with higher total basal area but smaller quadratic mean diameter than their pre-harvest analogues. As a result, none of the contemporary stands are within the HRV. Second, fire exclusion affected stand development by indirectly contributing to the persistence of high tree densities through time. In contrast, historical selective harvesting directly and immediately altered stand structure and composition by removing the largest fire-tolerant trees from stands, as well as shade-intolerant species. The interaction of these two factors produced stands dominated by shade-tolerant species that are denser than would have occurred otherwise. Third, the absence of western larch regeneration, dearth of ponderosa pine regeneration, and higher-than-expected mortality of the largest trees indicate that all trees in dense stands are

stressed. Consequently, shade-intolerant species and remnant biological legacies from historical stands may be absent or underrepresented in the future. These trends imply stands have shifted to an alternate state, and are less resistant and resilient to fire or other disturbances. Next, I explain these findings in deeper detail.

3.4.1 Temporal trends align with other forests in western North America

Historical reconstructions and trends in structural changes through time align with the outcomes of reconstructions from dry forests throughout the western U.S. In stark contrast to contemporary dense stands of Douglas-fir, prior to harvesting, open forests averaged 184 trees ha^{-1} and 20 $\text{m}^2 \text{ha}^{-1}$ of basal area; half of these trees were shade-intolerant species. These attributes are within the ranges of reconstructions in dry, mixed-conifer forests from the Rocky Mountains of Montana to the Sierra Nevada Mountains of California (e.g., 50-337 trees ha^{-1} , 5.8-53.9 $\text{m}^2 \text{ha}^{-1}$ of BA, 35-100% of trees were shade-intolerant; Naficy *et al.* 2010, Knapp *et al.* 2013, Brown *et al.* 2015, Collins *et al.* 2017, Battaglia *et al.* 2018). Moreover, studies in forests from northern Arizona to the Rocky Mountains and Pacific Northwest of the U.S. also found increases in average density (173-855%) and average basal area (104-356%), but decreases in average quadratic mean diameter (5-45% reduction) (Fulé *et al.* 1997, Sloan 1998, Camp 1999, Arno *et al.* 1999, Moore *et al.* 2004, Everett and Baumgartner 2007, Scholl and Taylor 2010, Knapp *et al.* 2013, Brown *et al.* 2015, Stephens *et al.* 2015, Collins *et al.* 2017, Battaglia *et al.* 2018).

The large increases in average stand density and reductions in quadratic mean diameter that I observed relative to other studies highlight the need to include overstory trees with small diameters in contemporary assessments and historical reconstructions. While the increase in contemporary basal area of 148% over pre-harvest levels was within the range of other studies,

deviations in average density (+1,463%) and average quadratic mean diameter (-63%) were greater than previously reported. These discrepancies are likely because I included trees with DBH <4 cm but height >1.3 m in reconstructions. My contemporary stands averaged 216% denser than the highest average stand density among the other studies (i.e., 1,265 trees per hectare; Fulé *et al.* 1997). Since other studies only included trees with DBH $\geq$ 9.14 cm (Moore *et al.* 2004, Knapp *et al.* 2013, Collins *et al.* 2017), shifting their minimum diameter limit to 4 cm would include smaller trees and inevitably increase their reconstructed densities.

Including small trees in contemporary and historical assessments provided unique insights into changes in stand structure. Small trees are often treated as components of the understory (e.g., DBH <10 cm; Knapp *et al.* 2013) and excluded from stand-level metrics of density, basal area, and quadratic mean diameter. My reconstructions confirmed that subcanopy layers (i.e., suppressed and intermediate canopy positions) were as old as some co-dominant trees, and age analyses revealed that small-diameter trees formed a large component of overstory cohorts (Chapter 2). Moreover, saplings contribute up to 61% of live-tree basal area and up to 58% of total (live and dead tree) basal area in contemporary stands, showing small trees can occupy substantial portions of available growing space. Although diameter limits in contemporary studies may be imposed by past decisions (i.e., Moore *et al.* (2004) resampled previously established plots with fixed lower diameter limits), and differences in site productivity can affect growth rates and necessitate variations in minimum DBH limits (e.g., maximum BA of 78.2 m² ha⁻¹ in contemporary stands in Knapp *et al.* 2013 versus 42.7 m² ha⁻¹ in this study), my reconstructions highlight benefits of including small trees in contemporary and historical assessments of stand structure.

Historical selective harvesting in my study area reduced the BA of shade-intolerant

species more than has been previously reported. While ponderosa pine and western larch are shade-intolerant, Douglas-fir is moderately-to-highly shade-tolerant (Parish *et al.* 1996, Klinka *et al.* 2003, Powell 2014), making it the most shade-tolerant species in my study. The proportion of BA occupied by Douglas-fir in my sites increased by 192%, on average, which is within the range of increases in BA of shade-tolerant trees reported in other studies (125-248%; Moore *et al.* 2004, Naficy *et al.* 2010, Knapp *et al.* 2013, Merschel *et al.* 2014, Collins *et al.* 2017). However, while other studies reported average stand-level reductions of 3-43% in the BA occupied by shade-intolerant species, the BAs of ponderosa pine and western larch were reduced by 53% and 67%, averaging a reduction of 60% in the BA of shade-intolerant trees in my stands.

Decreases in the abundance of shade-intolerant trees are typically attributed to fire exclusion, the removal of frequent surface fires that historically limited tree establishment and maintained low-density, open-canopied stands (Hessburg *et al.* 2015, Falk *et al.* 2019). However, selective harvesting also decreases shade-intolerant trees because it creates small canopy gaps that favor regeneration of shade-tolerant species (Hessburg and Agee 2003, Fitzgerald 2005, Naficy *et al.* 2010). Moreover, historical selective harvesting in my study area targeted large, shade-intolerant trees, which directly reduced their numbers and prevented their contributions to future seed pools. Although all contemporary stands have been affected by fire exclusion, the large reduction in BA of shade-intolerant trees that I observed is likely the result of intensive, unregulated selective harvesting throughout the early 20th century. While harvesting on public land in the U.S. has been regulated by the federal government since 1897 (e.g., Organic Administration Act of 1897; Bassman 1974), public forests in Canada are managed by the provinces, and there were no restrictions on the amount of timber harvested in British Columbia until establishment of the Annual Allowable Cut in 1949 (Drushka 1998, p.76-77; Environmental

Reporting BC 2020). Given the near complete removal of shade-intolerant trees from my study sites, I conclude harvesting outweighed fire exclusion to reduce the proportion of BA occupied by shade-intolerant species in the study area.

3.4.2 Harvesting and fire exclusion interacted to create dense stands

Stand histories prevent a comparative assessment of the individual contributions of historical selective harvesting versus fire exclusion in driving high stand densities. Other studies have reported contrasting influences of fire exclusion alone versus the interactions of fire exclusion and harvesting on stand structure and composition (Naficy *et al.* 2010, Knapp *et al.* 2013, Collins *et al.* 2017). While Naficy *et al.* (2010) concluded that logging in stands where fire was excluded promoted higher densities than fire exclusion alone, Knapp *et al.* (2013) and Collins *et al.* (2017) concluded that fire exclusion promoted higher stand densities. Two factors prevented this type of comparative analysis in my study: (1) fire was not immediately excluded as evidence by the fact that 40% of stands burned after they were first harvested; and (2) all stands were harvested. Instead of comparing the individual contributions of harvesting and fire exclusion in driving high stand densities, it is worth discussing how these factors and their interactions shaped stand structure, composition, and development in my study sites.

Documented historical timber harvesting corroborates my reconstructions of tree harvesting and confirms selective harvesting was the keystone process that removed large, fire-tolerant trees and shaped future stand structure and composition. In the 19th and early 20th centuries, technological limitations restricted logging operations to easily accessible terrain, often near perennial sources of water (**Table 3.6**). Consequently, the lowest elevation forests were harvested first, followed by forests in more remote locations. By 1930, most of the easily accessible trees were harvested (Turner 2010, p.47), and numerous fires burned large areas, most

of which were negligently set by the loggers themselves (Drushka 1998, p.77). Harvest dates derived from tree rings align with the documented timeline, as 80% of plots, including 100% of PP plots, were first harvested on or before 1922. All PP plots were harvested before the IDF plots due to their location in the lowest elevations, near water sources, and on gentle slopes or small hills in the valley bottom. Although IDF plots were generally further from lakes and rivers, most were easily accessible because they had gentle or moderate slopes. The four remaining plots with initial harvest dates after 1930 were relatively remote (IDFX07) or on steep slopes (34-45%; IDFX06, IDFX09, IDFX10). Additionally, IDFX07 burned in 1917, IDFX06 and IDFX09 burned in 1919, and all four plots burned in 1931 (Chapter 2), which likely deterred harvesting until later dates. The focused removal of large, fire-tolerant trees, particularly shade-intolerant species, directly and immediately lowered the resistance of stands to fires, reduced the contributions of shade-intolerant species to future populations, and released abundant growing space that contributed to the mass recruitment of regenerating shade-tolerant trees into overstories.

Fire exclusion outweighed harvesting in driving stand development and landscape-scale densification by removing fires that historically maintained the metastability of low density stands. The recruitment of regeneration into overstories through time provides a compelling narrative for the effects of fire exclusion on stand development. From Period 1 to Period 2 to contemporary reconstructions, regeneration numbers within stands decreased as regeneration was recruited into canopies, and stands became denser. Densification in the absence of fire highlight the effects of fire exclusion on forest development. Although historical fires, selective harvesting and their interactions initiated new tree establishment and influenced future stand composition, fire exclusion allowed regenerating trees to persist through time by removing fire as the keystone

mechanism of tree death and forest thinning. Not surprisingly, once fires were excluded, all stands reached the stem-exclusion stage of development within an average of 26 years after the last fire, whereby new tree recruitment into the overstory ceased (Chapter 2). Had fires continued burning at historical return intervals of 7-15 years, it is very likely that none of these stands would be dense.

Ineffective thinning treatments interacted with fire exclusion to perpetuate dense stands throughout the study area. Harvesting after 1951 focused on thinning small Douglas-fir trees to enhance the growth of residual trees. The unregulated and extensive removal of large trees by 1930 left very few options for harvesting in low-elevation forests throughout the study area. Moreover, stands became profusely dense in the absence of fire. To mitigate these effects, thinning projects were implemented in the study area from the 1970s to the 1990s to remove height-repressed trees in dense stands (B.J.R. Harris, *personal communication*, October 26, 2019). Reconstructions revealed that the basal area of contemporary stands increased after harvesting in Period 2, indicating thinning treatments may have enhanced the growth of residual trees. However, thinning only removed an average of $0.20 \text{ m}^2 \text{ ha}^{-1}$ of BA from stands in Period 2, and subsequent growth enhancements were spread over hundreds to thousands of residual trees per hectare. Consequently, thinning projects were largely ineffective, as they removed too few trees and too little basal area, failed to recruit regeneration into the overstory, and failed to transition stands out of the stem-exclusion stage of development. Interacting with fire exclusion, ineffective thinning treatments only served to perpetuate dense stands throughout the study area.

3.4.3 All contemporary stands exceed the Historical Range of Variability (HRV)

All contemporary dense stands exceeded HRV. Stands comprised of ponderosa pine and Douglas-fir (the driest stands) have departed the furthest from HRV. The large departures are

due to their location in easily accessible areas, which facilitated early and intensive harvesting in all ponderosa pine and Douglas-fir stands by 1922 (**Fig. 3.5**).

The baseline HRV reconstructions that I developed have potential applications in dense forests throughout the study area. The HRV framework provides empirical benchmarks for assessing degree of departures from ecosystem composition, structure, and function (Cissel *et al.* 1994, Morgan *et al.* 1994, Swanson *et al.* 1994). Numerous landscape-scale studies have reconstructed various components of the HRV for western North American forests (Keane *et al.* 2004, Hessburg *et al.* 2007, Keane *et al.* 2008). The greatest limitations of these large, spatial reconstructions are (a) the lack of adequate data to accurately represent the full range of variation in historical attributes for all components of a landscape, and (b) the scalability of stand attributes to such a large area (Keane *et al.* 2009). To address the landscape scales, I implemented a stratified-random sampling design to ensure my study plots were statistically representative of Douglas-fir, ponderosa pine and/or western larch stands with >25% crown closure, and densities >400 live trees ≥ 12.5 cm dbh, or >800 live and dead trees >1.3 m height ha^{-1} throughout the study area. As such, my detailed stand-level results are valid for and applicable to the dense forests throughout the study area.

3.4.4 Trends in regeneration and tree mortality indicate low resilience

Novel reconstructions of historical regeneration indicate shade-intolerant species may be extirpated from my study sites without human intervention. Documentation of regeneration trends is critical for understanding the future trajectory of dry forests. Although numerous studies document regeneration in contemporary stand reconstructions, few retrospective studies have quantified regeneration densities and composition in historical reconstructions (Everett and Baumgartner 2007, Knapp *et al.* 2013). While Knapp *et al.* (2013) reconstructed regeneration

attributes from historical surveys, Everett and Baumgartner (2007) used a dendroecological approach; however, regeneration and saplings were combined in a category of understory trees with DBH <7.6 cm. To my knowledge, the present study represents the first dendroecological attempt to distinguish regeneration from saplings in historical reconstructions.

Despite it being impossible to know exactly how much regeneration was present in historical reference years (Daniels *et al.* 2017), the trends in my reconstructions raise concerns. Reconstructions in contemporary stands show a 73% reduction in overall seedling survival since Period 1. Commensurate with reduced regeneration density is a reduction in shade-intolerant species, which decreased from 30% in Period 1 to only 0.3% in contemporary stands, representing a 99% reduction in regeneration of these species. Moreover, western larch regeneration was completely absent from contemporary stands. These trends are testament to increasing stand densities over time, resulting from the interactions of fire exclusion and historical selective harvesting that have reduced regeneration of all species and precluded western larch regeneration. Without human intervention, the deep-shaded understory of these dense stands may preclude western larch and ponderosa pine from future forests.

Dead trees of all size classes indicate all trees are stressed, but higher-than-expected proportions of dead large trees indicates an active shift to an alternate state. Density-dependent mortality affects smaller trees in dense stands (Oliver and Larson 1996). Indeed, 89% of dead trees were small (DBH <12.5 cm), and density-dependent mortality occurred in nearly all plots (except IDFX12). However, 11% of dead trees were larger (DBH ≥12.5 cm), and greater proportions of dead trees were large, rather than small, in two plots (≥24% in IDFX04 and IDFX12). It is possible that the abundant smaller trees outcompete larger trees for water and drive large tree mortality (e.g., inverse (a) symmetric competition defined by Biondi, 1996), but

additional research is needed to assess this hypothesis. Nevertheless, mortality trends indicate large trees are stressed and dying in contemporary dense stands, and forests appear to be shifting to an alternate state comprised of high numbers of small, fire-intolerant but shade-tolerant trees.

3.5 Conclusions

This study confirms a troubling trend in dry forests of southeastern BC that is widespread in the dry forests of western North America. Through historical selective harvesting and fire exclusion, compounded by climate change and a broad range of other forest management and land-use practices, humans have directly and indirectly caused dramatic shifts in dry forest structures and composition over a short period of 100-150 years. These changes have occurred most rapidly in areas that were intensively settled by Europeans, areas that were also home to Indigenous people who actively managed and maintained the forests for hundreds to thousands of years (Chapter 2). This study has revealed that it has taken less than 150 years to push these forests outside their HRV and degrade their resilience to fire and other disturbances. Human intervention to restore ecosystem composition and structure would enhance forest resilience to future drought and fires.

3.6 Tables

Table 3.1 Summary of stump surveys and harvest reconstructions in 20 plots in dense forests in southeastern BC.

Species are Douglas-fir (PSME), ponderosa pine (PIPO), and western larch (LAOC). Diameter at breast height (DBH) classes are sapling (S), pole (P), mature (M), and dominant (D).

Plot	n (ha ⁻¹)	Species			Decay Class				Living Stumps n	Reconstructed DBH Classes				Stump samples n	Harvest dates
		PSME	PIPO	LAOC	1	2	3	4		S	P	M	D		
PPX02	138	116	22	0	34	20	74	10	26	18	54	46	20	10	1917, 1959
PPX03	18	2	16	0	0	0	14	4	0	0	0	0	18	2	1922
PPX04	330	302	28	0	40	52	188	50	20	36	96	106	92	9	1912, 1962, 1976
PPX07	196	152	44	0	42	24	126	4	48	2	84	40	70	9	1907, 1927, 1955, 1963
PPX08	276	240	36	0	10	20	202	44	12	74	90	36	76	13	1912, 1969, 1994
PPX09	214	84	130	0	6	50	154	4	4	24	22	32	136	11	1915, 1966
PPX10	162	72	22	68	6	22	116	18	8	4	30	28	100	10	1917, 1951, 1980
IDFX02	66	34	0	32	4	6	42	14	8	0	0	16	50	8	1909, 1953, 1964, 1971
IDFX03	180	22	158	0	0	0	126	54	0	0	0	50	130	5	1922
IDFX04	154	88	6	60	2	0	114	38	2	0	36	48	70	8	1917, 1978
IDFX05	140	116	0	24	14	0	64	62	16	6	10	18	106	6	1907, 1939
IDFX06	50	24	0	26	0	6	38	6	2	0	2	4	44	8	1964
IDFX07	124	20	0	104	0	0	110	14	8	0	0	44	80	8	1937
IDFX08	162	94	0	68	0	0	88	74	0	0	0	16	146	7	1914
IDFX09	70	26	0	44	0	0	40	30	4	0	0	20	50	8	1942
IDFX10	70	8	0	62	0	0	68	2	6	0	0	0	70	6	1949
IDFX11	124	86	24	14	22	10	70	22	24	32	38	4	50	9	1919, 1959, 1968
IDFX12	118	82	10	26	0	0	102	16	0	0	0	14	104	4	1919, 1949
IDFX13	98	56	0	42	0	0	80	18	0	0	0	2	96	8	1922
IDFX14	58	26	4	28	2	12	38	6	6	0	4	4	50	8	1919, 1943, 1977, 1986

Table 3.2 Fire history derived from plot-level fire-scar records.

Metrics include mean and maximum (max) fire return intervals (FRI) and time since the last fire (TSLF) in years. The number of missed fires in period 1 (P1), period 2 (P2) and contemporary (C) forests were estimated for reconstructed start years for each period, and calculated as the number of years that transpired since the last fire, divided by the plot-level mean fire return interval.

Plot	Last Fire	Mean FRI	Max FRI	TSLF	Missed Fires		
					P1	P2	C
PPX02	1895	7.0	70	118	3.1	9.1	16.9
PPX03	1889	11.4	32	124	2.9	-	10.9
PPX04	1919	10.3	32	94	-	4.2	9.1
PPX07	1889	9.0	28	124	2.0	7.3	13.8
PPX08	1889	13.9	48	124	1.7	5.8	8.9
PPX09	1915	9.4	16	98	-	5.4	10.4
PPX10	1931	9.2	21	82	-	5.3	8.9
IDFX02	1873	14.0	34	140	2.6	5.7	10.0
IDFX03	1923	13.1	34	90	-	-	6.9
IDFX04	1931	11.6	45	82	-	4.1	7.1
IDFX05	1920	10.8	21	93	-	-	8.6
IDFX06	1965	14.0	37	48	-	-	3.4
IDFX07	1935	9.8	27	78	0.2	-	8.0
IDFX08	1909	12.6	51	104	0.4	-	8.3
IDFX09	1931	13.6	29	82	0.8	-	6.0
IDFX10	1946	13.1	50	67	0.2	-	5.1
IDFX11	1909	10.5	26	104	1.0	4.8	9.9
IDFX12	1926	11.6	34	87	-	-	7.5
IDFX13	1942	11.9	22	71	-	-	6.0
IDFX14	1905	14.9	33	108	0.9	4.8	7.2

Table 3.3 Plot-level stand structures for Period 1, Period 2 and Contemporary forests.

Year indicates the reference years in Periods 1 and 2 for attributes reconstructed using tree rings; contemporary attributes were measured in 2013. Attributes include tree density, basal area (BA) and quadratic mean diameter (QMD). Snags and Harvested indicate the density and basal area of dead trees that were present in each reference year, or were cut in Periods 1 and 2.

Plot	Period 1										Period 2										Contemporary					
	Year	Regen (n ha ⁻¹)	Live trees (ha ⁻¹)			Snags (ha ⁻¹)		Harvested (%)		Year	Regen (n ha ⁻¹)	Live trees (ha ⁻¹)			Snags (ha ⁻¹)		Harvested (%)		Regen (n ha ⁻¹)	Live trees (ha ⁻¹)			Snags (ha ⁻¹)			
			Density	BA	QMD	Density	BA	Density	BA			Density	BA	Density	BA	Density	BA	Density		BA	Density	BA	QMD	Density	BA	
PPX02	1917	862	109	10.1	34.4	1	0.3	77	86	1959	28	941	8.7	10.9	1	0.3	6	5	5034	874	18.5	16.4	192	2.5		
PPX03	1922	1206	76	6.4	32.8	0	0.0	24	66	-	-	-	-	-	-	-	-	1867	1054	31.1	19.4	271	0.7			
PPX04	1912*	4262	248	31.0	39.9	0	0.0	96	99	1962	73	3872	11.4	6.1	492	0.5	2	14	0	2018	22.8	12.0	2327	2.7		
PPX07	1907	1613	281	25.5	34.0	0	0.0	46	90	1955	211	2047	10.8	8.2	0	0.0	3	6	0	1646	27.9	14.7	547	1.8		
PPX08	1912	1230	268	17.0	28.4	0	0.0	91	97	1969	0	2196	20.1	10.8	50	0.3	1	3	267	1994	40.7	16.1	222	0.7		
PPX09	1915	5910	183	26.9	43.4	0	0.0	87	99	1966	32	6643	9.1	4.2	0	0.0	1	4	0	6067	27.3	7.6	551	0.3		
PPX10	1917*	0	354	29.9	32.8	0	0.0	38	89	1980	1729	833	19.4	17.2	0	0.0	3	3	400	2328	34.4	13.7	206	0.6		
IDFX02	1909	4456	235	14.9	28.4	0	0.0	25	94	1953	0	4557	19.7	7.4	86	0.0	0.2	2	0	3827	41.2	11.7	806	1.2		
IDFX03	1922*	18826	191	20.7	37.2	0	0.0	94	98	-	-	-	-	-	-	-	-	0	14219	37.5	5.8	4720	4.7			
IDFX04	1917*	5	165	13.9	32.8	0	0.0	92	95	1978	1246	281	8.3	19.4	0	0.0	1	0.3	4567	1473	19.0	12.8	77	1.0		
IDFX05	1907*	35	151	19.2	40.2	0	0.0	93	98	-	-	-	-	-	-	-	-	34	2316	40.4	14.9	1687	3.2			
IDFX06	-	-	-	-	-	-	-	-	-	1964*	6335	270	11.6	23.4	0	0.0	19	59	0	3343	39.0	12.2	3215	5.7		
IDFX07	1937	320	184	16.7	34.0	0	0.0	67	83	-	-	-	-	-	-	-	-	0	1446	32.2	16.8	1040	1.7			
IDFX08	1914	1045	162	30.5	49.0	0	0.0	100	100	-	-	-	-	-	-	-	-	67	1004	24.5	17.6	844	3.3			
IDFX09	1942	445	151	11.6	31.4	0	0.0	46	57	-	-	-	-	-	-	-	-	1200	1636	25.9	14.2	236	0.7			
IDFX10	1949	3134	143	21.0	43.3	2	0.2	49	77	-	-	-	-	-	-	-	-	34	2468	22.2	10.7	989	1.7			
IDFX11	1919	945	162	19.9	39.6	0	0.0	57	73	1959	2840	543	9.8	15.2	0	0.0	6	2	0	2786	38.9	13.3	566	1.2		
IDFX12	1919*	0	185	28.7	44.4	0	0.0	64	93	-	-	-	-	-	-	-	-	34	1163	19.7	14.7	1	0.1			
IDFX13	1922*	83	130	23.9	48.4	0	0.0	75	95	-	-	-	-	-	-	-	-	0	1078	34.0	20.0	383	1.0			
IDFX14	1919	2380	127	15.8	39.8	0	0.0	35	74	1977	0	2329	17.4	9.8	226	0.2	0.6	6	0	1852	28.4	14.0	691	2.6		

* Plots burned after reconstruction years

Table 3.4 Comparisons of stand structures in Period 1 (P1), Period 2 (P2) and contemporary (C) forests.

T-test statistics (P-values) are given for pairwise comparisons between time periods for the density, quadratic mean diameter (QMD), and basal area (BA) of all live trees (height > 1.3 m) and BA of live trees stratified by size (sapling, pole, mature and dominant classes). Bold values were significant when $\alpha = 0.05$.

Stand structure attribute	Temporal comparisons		
	Period 1 v Period 2	Period 1 v Contemporary	Period 2 v Contemporary
Density (trees ha ⁻¹)	-3.423 (0.008)	3.803 (<0.0001)**	-0.446 (0.661)
QMD (cm ha ⁻¹)	10.898 (<0.0001)	14.353 (<0.0001)	-1.064 (0.307)
Basal area (m ² ha ⁻¹)			
All trees	2.501 (0.024)	-3.967 (0.0003)	-5.883 (<0.0001)
Sapling	-3.465 (0.007)	3.724 (0.0002)**	0.092 (0.927)
Pole	-5.27 (0.0003)	-11.514 (<0.0001)*	-2.273 (0.037)
Mature	-1.448 (0.173)*	-11.259 (<0.0001)*	-4.864 (0.0002)
Dominant	5.87 (<0.0001)	4.626 (<0.0001)	-1.505 (0.15)

* data were log transformed ($\text{LN}(x + 1)$) to meet assumptions of normality

** significance was assessed using a Wilcoxin Signed-Rank Test: Z-test statistic (P-value) are provided

Table 3.5 Assessment of departures from the historical range of variation (HRV) of stand structures and species composition for plots stratified by composition. Species assemblages include combinations of ponderosa pine (PIPO), Douglas-fir (PSME) and western larch (LAOC). For each metric, 0/1 indicate values in contemporary stands that are outside/within HRV, with the sums of scores determining the category and degree of departure. Contemporary stands with a category of “Transitional” have a score > 0% but < 100%, whereas stands with a category of “Outside” have a score of 0%. The degree of departure is either High (score ≤ 33%), Moderate (score 34–66%), or Low (score > 66%).

Species Assemblage	Plot	Stand			Species						Score Total	Score Percentage	HRV Category	Degree of Departure
					PSME		PIPO		LAOC					
		Density	BA	QMD	Density	BA	Density	BA	Density	BA				
PIPO-PSME	PPX02	0	1	0	0	1	1	0	-	-	3	43%	Transitional	Moderate
	PPX03	0	0	0	0	0	0	1	-	-	1	14%	Transitional	High
	PPX04	0	1	0	0	0	0	0	-	-	1	14%	Transitional	High
	PPX07	0	1	0	0	1	0	1	-	-	3	43%	Transitional	Moderate
	PPX08	0	0	0	0	1	0	0	-	-	1	14%	Transitional	High
	PPX09	0	1	0	0	0	0	0	-	-	1	14%	Transitional	High
	IDFX03	0	0	0	0	0	0	0	-	-	0	0%	Outside	High
LAOC-PSME	IDFX05	0	0	0	0	0	-	-	0	1	1	14%	Transitional	High
	IDFX06	0	0	0	0	0	-	-	1	1	2	29%	Transitional	High
	IDFX08	0	1	0	0	1	-	-	0	1	3	43%	Transitional	Moderate
	IDFX10	0	1	0	0	1	-	-	0	1	3	43%	Transitional	Moderate
	IDFX13	0	0	0	0	0	-	-	1	1	2	29%	Transitional	High
LAOC-PIPO-PSME	PPX10	0	0	0	0	0	0	1	0	1	2	22%	Transitional	High
	IDFX02	0	0	0	0	0	1	1	0	0	2	22%	Transitional	High
	IDFX04	0	1	0	0	1	0	0	0	0	2	22%	Transitional	High
	IDFX07	0	0	0	0	0	1	1	1	0	3	33%	Transitional	Moderate
	IDFX09	0	1	0	0	0	1	1	1	0	4	44%	Transitional	Moderate
	IDFX11	0	0	0	0	0	1	1	0	0	2	22%	Transitional	High
	IDFX12	0	1	0	0	1	1	1	1	0	5	56%	Transitional	Moderate
	IDFX14	0	1	0	0	0	1	1	0	0	3	33%	Transitional	Moderate

Table 3.6 The types, limitations, and application of different methods of log skidding and transportation in the study area.

Log Skidding/Transport type	Limitation	Application in study area	Source
Horse skidding	Maximum slopes of 28% to operate safely	Primary method	Wang 1997, Drushka 1998
Mechanized skidding and cable yarding	Steam donkeys: distance $\leq 150\text{m}$ from landings Cable yarding: distance $\leq 500\text{m}$ (1000m maximum on level ground) from landings	Used by one company	Drushka 1998
Flumes from site to rivers/lakes	Proximity to water source	Alternate method (several built)	Drushka 1998
Water transport to mills	Proximity to rivers and lakes	Primary for sites near water (most PP sites)	Turner 2010
Rail transport to mills	Main lines: maximum slopes of 2-3% Spur lines: slopes $\leq 5-6\%$ common (maximum slopes of 7-8%)	Primary for sites away from water (most IDF sites)	Turner 2010

3.7 Figures

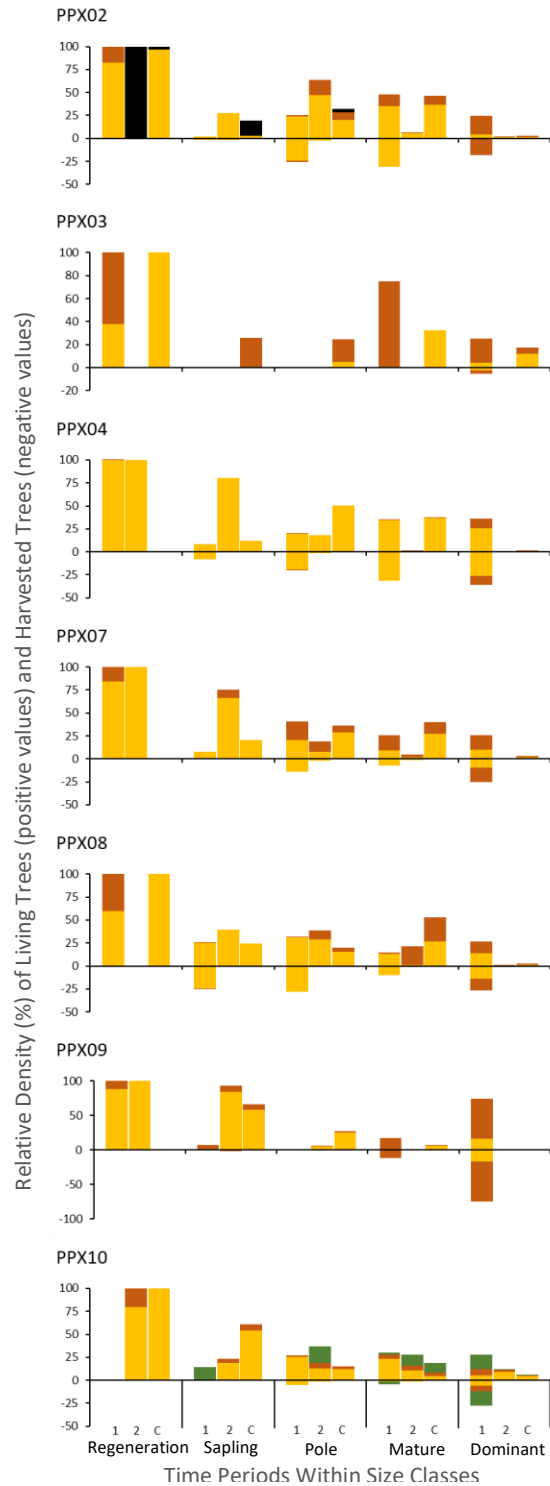


Figure 3.1a Changes through time in the density of trees by size class in PP Plots.

Along the x-axis, time periods are within size classes. Time periods are Period 1 (1), Period 2 (2), and Contemporary (C). Size classes are regeneration (Regen; height ≤ 1.3 m), sapling (height > 1.3 m, DBH < 7.5 cm), pole ($7.5 \text{ cm} \leq \text{DBH} < 12.5$ cm), mature ($12.5 \text{ cm} \leq \text{DBH} < 30$ cm), and dominant (DBH ≥ 30 cm). Species are Douglas-fir (yellow), ponderosa pine (red), western larch (green), and all other species (black). Regeneration and tree densities in each period are in Table 3.3.

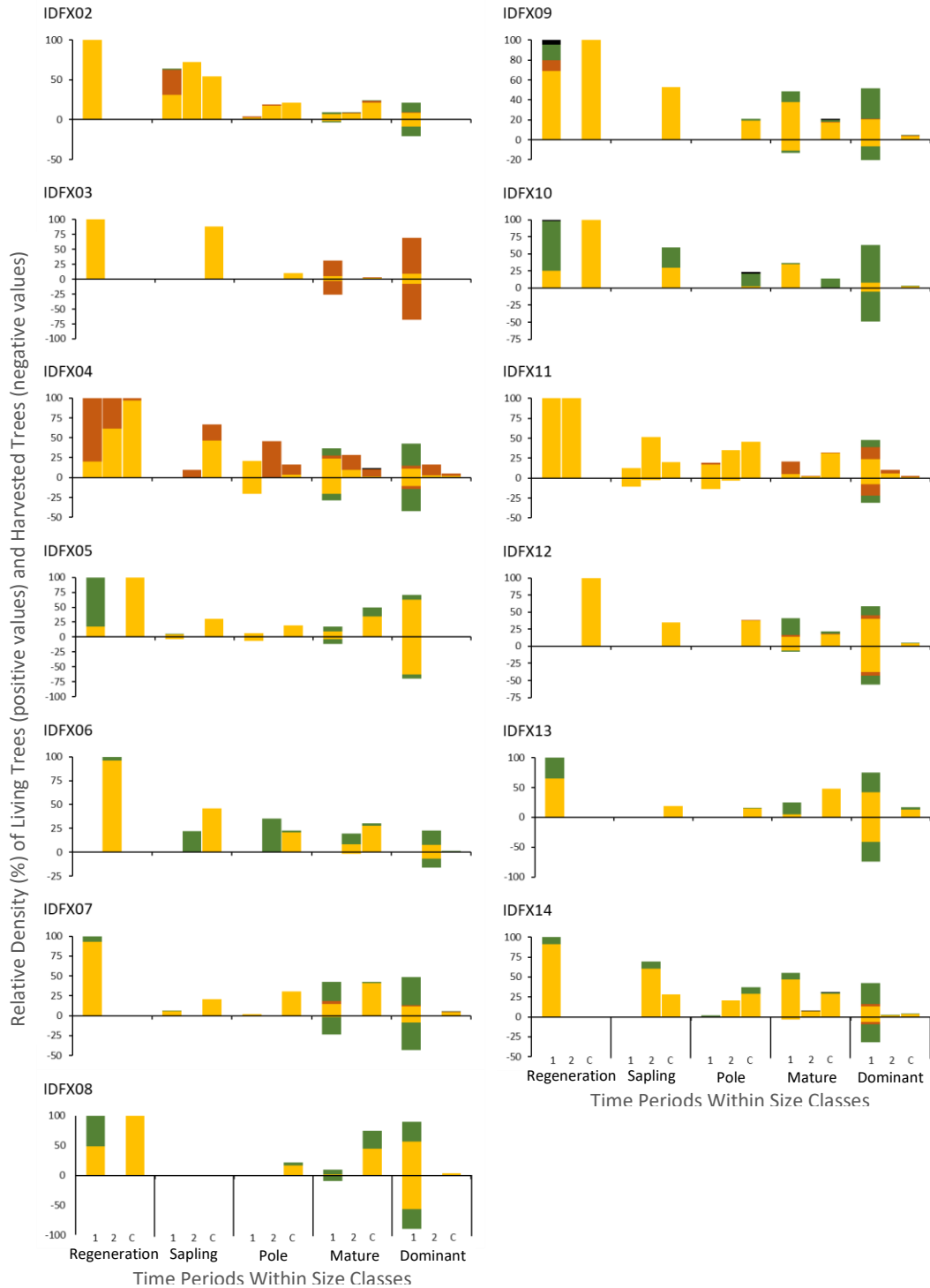


Figure 3.1b Changes through time in the density of trees by size class in IDF Plots. Along the x-axis, time periods are within size classes.

Time periods are Period 1 (1), Period 2 (2), and Contemporary (C). Size classes are regeneration (Regen; height ≤ 1.3 m), sapling (height > 1.3 m, DBH < 7.5 cm), pole ($7.5 \text{ cm} \leq \text{DBH} < 12.5$ cm), mature ($12.5 \text{ cm} \leq \text{DBH} < 30$ cm), and dominant (DBH ≥ 30 cm). Species are Douglas-fir (yellow), ponderosa pine (red), western larch (green), and all other species (black). Regeneration and tree densities in each period are in Table 3.3.

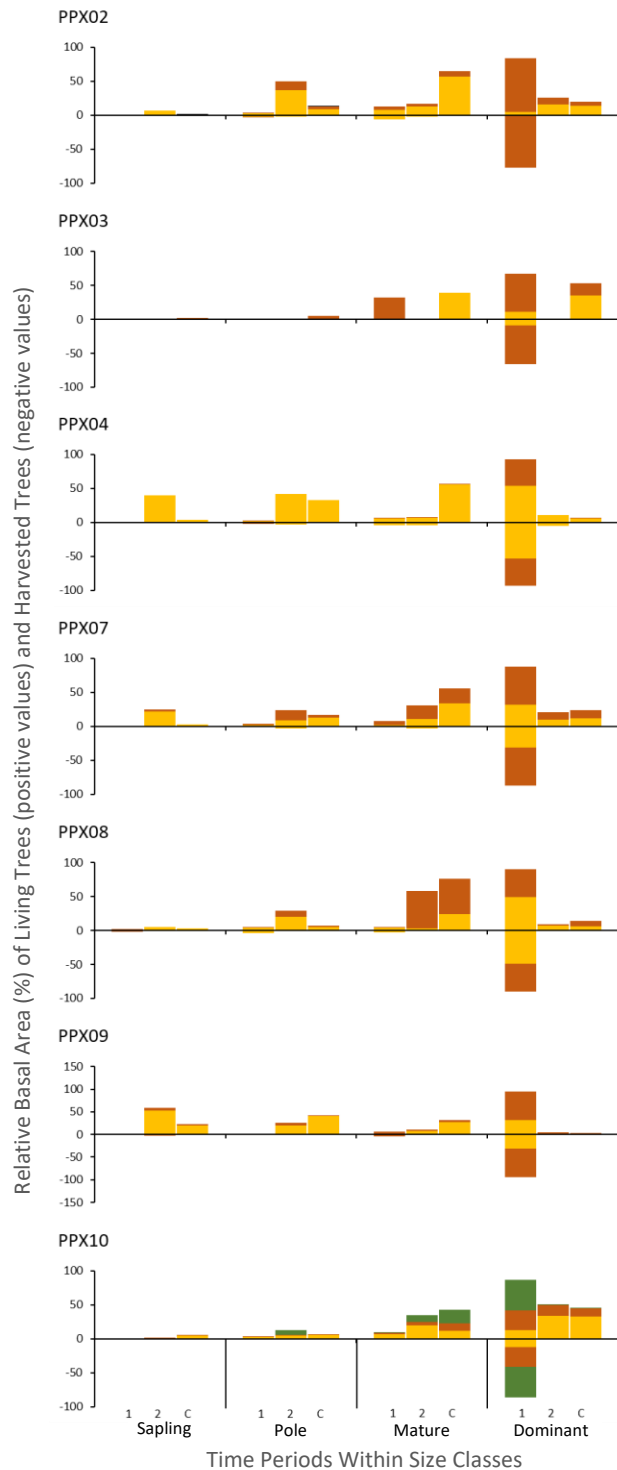


Figure 3.2a Changes through time in the basal area of trees by size class in PP Plots. Along the x-axis, time periods are within size classes.

Time periods are Period 1 (1), Period 2 (2), and Contemporary (C). Size classes are regeneration (Regen; height ≤ 1.3 m), sapling (height > 1.3 m, DBH < 7.5 cm), pole ($7.5 \text{ cm} \leq \text{DBH} < 12.5$ cm), mature ($12.5 \text{ cm} \leq \text{DBH} < 30$ cm), and dominant (DBH ≥ 30 cm). Species are Douglas-fir (yellow), ponderosa pine (red), western larch (green), and all other species (black). Basal areas in each period are in Table 3.3.

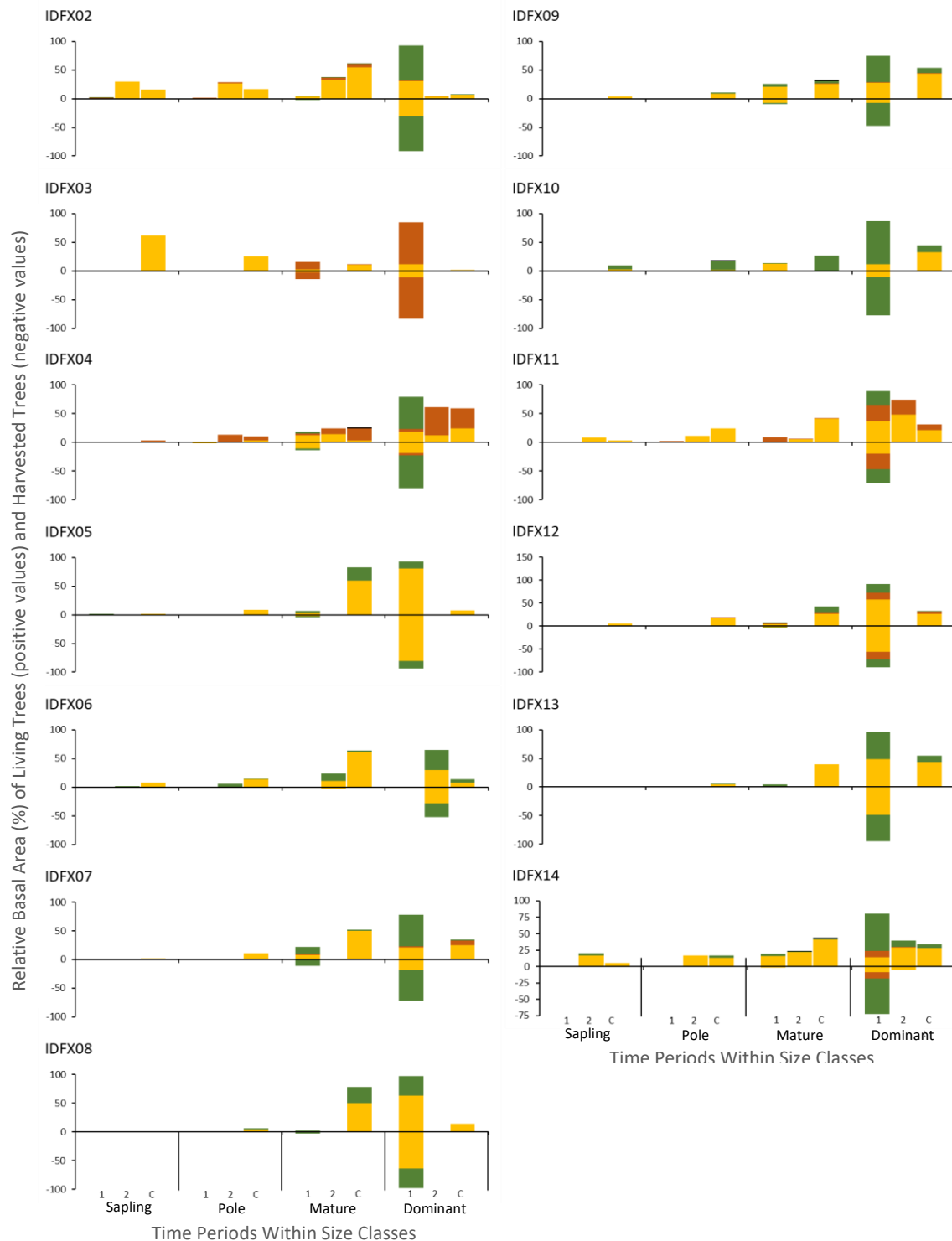


Figure 3.2b Changes through time in the basal area of trees by size class in IDF Plots. Along the x-axis, time periods are within size classes.

Time periods are Period 1 (1), Period 2 (2), and Contemporary (C). Size classes are regeneration (Regen; height ≤ 1.3 m), sapling (height > 1.3 m, DBH < 7.5 cm), pole ($7.5 \text{ cm} \leq \text{DBH} < 12.5$ cm), mature ($12.5 \text{ cm} \leq \text{DBH} < 30$ cm), and dominant (DBH ≥ 30 cm). Species are Douglas-fir (yellow), ponderosa pine (red), western larch (green), and all other species (black). Basal areas in each period are in Table 3.3.

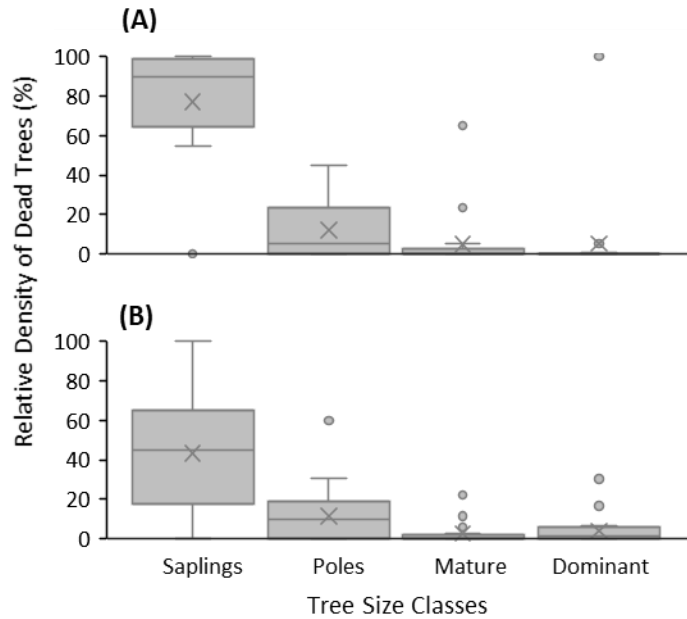


Figure 3.3 Distribution of the density of dead trees across size classes in contemporary stands.

Distributions reflect (A) the proportion of dead trees by size class in each stand (e.g., for saplings, the proportion of dead saplings to all dead trees in each stand), and (B) the proportion of dead trees to all live and dead trees of each size class in each stand (e.g., for saplings, the proportion of dead saplings to the total number of live and dead saplings in each stand). Size classes are sapling (height >1.3 m, DBH < 7.5 cm), pole (7.5 cm ≤ DBH < 12.5 cm), mature (12.5 cm ≤ DBH < 30 cm), and dominant (DBH ≥ 30 cm). In each box plot, the horizontal line represents the median, “X” represents the mean, box boundaries are the 25th and 75th percentiles, whiskers are the 5th and 95th percentiles, and dots are outliers.

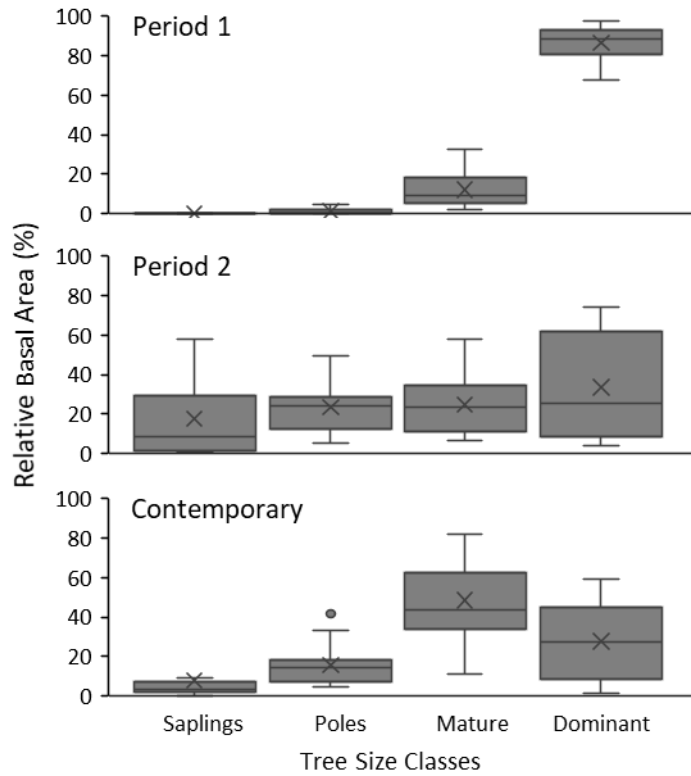


Figure 3.4 Changes in the distribution of stand-level basal area of live trees across size classes through time.

Size classes are regeneration (Regen; height ≤ 1.3 m), sapling (height > 1.3 m, DBH < 7.5 cm), pole ($7.5 \text{ cm} \leq \text{DBH} < 12.5$ cm), mature ($12.5 \text{ cm} \leq \text{DBH} < 30$ cm), and dominant (DBH ≥ 30 cm). In each box plot, the horizontal line represents the median, “X” represents the mean, box boundaries are the 25th and 75th percentiles, whiskers are the 5th and 95th percentiles, and dots are outliers.

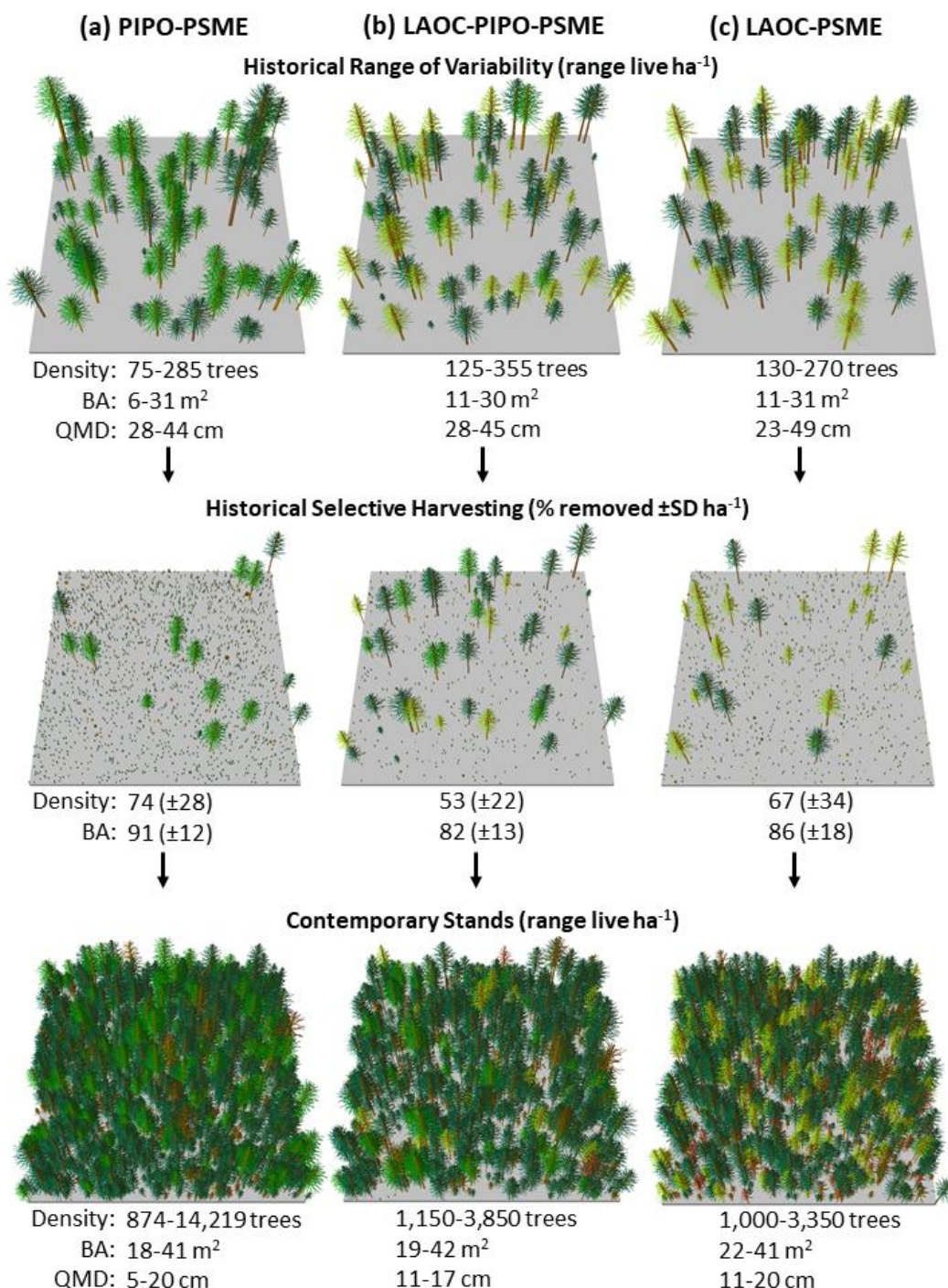


Figure 3.5 Historical range of variability of dry forests stands and changes through time following European settlement.

Images depict average structure and composition for stands under the historical range of variability, following historical selective harvesting, and for contemporary conditions. Reconstructions are for stands with the following species assemblages (a) ponderosa pine and Douglas-fir (PIPO-PSME), (b) western larch, ponderosa pine and Douglas-fir (LAOC-PIPO-PSME), and (c) western larch and Douglas-fir (LAOC-PSME). Live/dead ponderosa pine, Douglas-fir and western larch are light green/light brown, dark green/dark brown, and yellow-green/red, respectively. Average regeneration densities are depicted on the surface of selectively harvested stands.

Chapter 4: Sub-canopy trees outcompete canopy-dominant trees in dense dry forests of British Columbia

4.1 Introduction

Western North American forests are increasingly stressed by extreme temperatures, droughts, fires, and insect outbreaks (Jolly *et al.* 2015, Abatzoglou and Williams 2016, Schoennagel *et al.* 2017, Serra-Diaz *et al.* 2018, Mathews 2020). Unfortunately, rates of environmental change are exceeding the capacity of forests to adapt (Allen *et al.* 2010, Carnicer *et al.* 2011, Stevens-Rumann *et al.* 2018, Anderegg *et al.* 2019). Consequently, human intervention is needed to reduce stress and enhance the resilience of forests where disturbance regimes have been disrupted and the historical range of variability is exceeded (Hessburg *et al.* 2019). Ecological restoration is a viable tool to achieve these goals (Hessburg *et al.* 2015, Stephens *et al.* 2021). However, knowledge regarding the sources and thresholds of stress is limited, which hinders the effectiveness of restoration treatments.

In forests, stress has been quantified in several ways. Decline in growth and increases in mortality are common indicators of stress that result from intense competition at the tree and stand scales, and climate-mediated resource limitations at regional to global scales (Oliver and Larson 1996, Pedersen 1998, Allen *et al.* 2010, Carnicer *et al.* 2011, Anderegg *et al.* 2019). At the tree-level, reduced growth and mortality are autogenic processes of stand development that result from trees differentiating into separate canopy positions over time, creating a hierarchy that determines access to limiting resources (Oliver and Larson 1996). The growth of overtopped trees declines and these trees eventually die as they are outcompeted for sunlight, water, and nutrients. During the stem-exclusion stage of stand development, trees experience density-

dependent stress as growing space becomes maximized and crowding instigates intense differentiation, causing declines in growth and increases in mortality (Oliver and Larson 1996). Trees in dense forests growing in dry climates are stressed by competition for both sunlight and water. Working in Arizona, where soil moisture limits tree growth, Biondi (1996) found evidence for inverse size-asymmetric competition, where high densities of small pines collectively outcompeted large pines for water, causing decreased basal area increment and increased mortality of large pines. This competitive effect may augment the effects of high temperatures and severe droughts in driving high levels of background mortality and forest die off, as has been observed at regional and global scales (van Mantgem *et al.* 2009, Allen *et al.* 2010, Carnicer *et al.* 2011).

In temperate forests, the dimensions of annually-formed tree rings reflect resource availability (Fritts 1976). When growth is limited, rings may be narrow, incomplete, or not formed for one or more years (i.e., missing). Within trees, missing rings typically occur near the base of the stem (Turberville and Hough 1939, Novak *et al.* 2011), due to higher rates of cambium production near the crown (Forest *et al.* 2006) and allocation of carbon to radial growth beginning at the top of the tree and progressing down the stem during the growing season (Larson 1969, Oliver and Larson 1996). Thus, missing rings are a local phenomenon limited primarily to the lower stem (Novak *et al.* 2011), and are more common during periods of suppressed growth (Lorimer *et al.* 1999, Novak *et al.* 2011, Leland *et al.* 2016). Missing rings associated with the canopy position of a tree are due to diminishing amounts of sunlight in lower strata, which reduces growth (Oliver and Larson 1996). Consequently, higher percentages of rings are missed among trees in suppressed and intermediate canopy positions than dominant and co-dominant positions (Lorimer *et al.* 1999). The frequency of missing rings also increases in

response to climatic variation and change. Novak *et al.* (2016a) found that the frequency of missing rings was positively correlated with high temperatures and low precipitation, both of which limit growth during dry years. Acute annual climatic events, such as extremely high temperatures and severe droughts, can prevent trees from producing a ring entirely (Novak *et al.* 2011).

The forests of the southern Rocky Mountain Trench, British Columbia include 80,000 ha of closed-canopied, mixed-conifer stands in which many canopy-dominant trees are declining and dying (Chapters 2 and 3). These stands currently contain 800 to over 18,000 live and dead trees ha⁻¹, although they established more than 100 years ago. Historical reconstructions show these stands are an artefact of disrupted surface-fire regimes and early 20th century logging (Chapter 2), making them candidates for ecological restoration to decrease stress to canopy-dominant trees and increase forest productivity (Chapter 3). The goal of this study was to examine the sources and thresholds of stress in canopy-dominant Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco var. *glauca* [Beissn.] Franco), ponderosa pine (*Pinus ponderosa* Douglas ex Laws.), and western larch (*Larix occidentalis* Nutt.) trees. I surveyed live and dead trees in 20 stands and conducted tree-ring analyses to reconstruct stand structure, composition, and the growth and death patterns of canopy dominant, co-dominant, intermediate, and suppressed trees during the stem exclusion stage of stand development. Using decline in growth, missing rings, and tree death as indicators of stress, my objectives were to determine if: (1) canopy-dominant trees experienced greater stress than trees in lower canopy positions; (2) stress in canopy-dominant trees was driven by climate or stand dynamics; and (3) the causes of stress differed among canopy-dominant species. By determining the causes of stress among canopy-dominant trees, the outcomes of this research can be applied to help practitioners identify and

prioritize forests for ecological restoration, and determine the type and frequency of treatments needed to enhance forest resilience to future change.

4.2 Methods

4.2.1 Study area and research design

This study was conducted in the southern Rocky Mountain Trench (RMT) located in southeastern British Columbia, Canada (Chapter 1). The research design is described in Chapter 2.

4.2.2 Data collection

One-hectare plots were established in homogeneous portions of each of the 20 stands. I censused all canopy-dominant trees, those with crown tops extending ≥ 1 m above the general canopy, in each plot and recorded species, DBH, and condition (live, dead). Smaller trees were sampled in subplots centered on randomly selected canopy-dominant trees; the number of subplots per plot reflected the number of species on the canopy-dominant stratum. An 11.28 m-radius plot (0.04 ha) was placed around selected canopy-dominant trees; in one stand with density $>18,000$ trees ha^{-1} , an 8m-radius plot (0.02 ha) was used. In each subplot, I recorded the species, condition (live, dead), DBH and height class (i.e., dominant, co-dominant, intermediate, and suppressed) of each tree. To reconstruct growth trends, establishment, and death dates, I sampled increment cores from all live and dead canopy-dominant trees in the 1-ha plot. Trees in other height classes were stratified by diameter following standard forestry practice in British Columbia (DBH ≥ 30 cm, 12.5–29.9 cm, 7.5–12.49 cm, <7.5 cm and >1.3 m height; BC MoFLNRORD 2018) and the 10 live or dead trees in each diameter class that were closest to plot centres were cored. When decayed trees were encountered, the next nearest tree in the same size class was selected for coring. For each sampled tree with DBH ≥ 12.5 cm, I extracted two

opposing cores within 30 cm of the ground. Multiple cores were extracted to ensure rings were within 10 rings of pith. For trees <12.5 cm DBH, full cross-sections were cut within 5 cm of the ground. The height and diameter of cores or cross-sections were recorded for all sampled trees.

4.2.3 Dendrochronological analyses

Samples were air dried, sanded until the cell structure was visible, and a digital image was created by scanning at 2400 or 4800 dpi for large or smaller samples, respectively. For cross-sections, two opposing radii were scanned to emulate sampling two cores per tree. Ring widths in all scanned images were measured to the nearest 0.001 mm using the program CooRecorder (v9.0, Cybis Elektronik 2018). Calendar years were assigned to tree rings by visually cross-dating ring widths and cross-correlation of measured ring-width series using CDendro (v9.0, Cybis Elektronik 2018). All samples were cross-dated to ensure the calendar years of rings were accurate, and years with missing or locally absent rings were recorded for each sample.

Years of tree death were determined from cross-dated outer-ring dates of dead trees, and years of establishment of living and dead trees were calculated from cross-dated pith or inner-ring dates. A geometric correction was applied to estimate the number of missing rings for the subset of increment cores that did not intercept the pith (Duncan 1989). Species-specific regressions were developed to determine the number of years for trees to grow to sample height ($r^2 = 0.89\text{--}0.93$, SEE = 2.81–7.78 years; Appendix 4.1) and applied to all increment cores and disks (Villalba and Veblen 1997, Wong and Lertzman 2001). The year of establishment for each tree was calculated as the inner-ring date minus the corrections for missed rings and sample height (Daniels *et al.* 2017).

To quantify growth trends, I reconstructed basal area increment (BAI), which provides a

biologically meaningful representation of growth trends that are independent of tree age, assuming stem growth is concentric (Biondi & Qaedan 2008). Because tree growth is often asymmetrical, the cross-dated rings from opposing radii were averaged to derive a single ring-width series for each tree, which was converted to BAI using the following equation:

$$BAI_t = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where r_t corresponds to the tree radius at DBH at end of year t , and r_{t-1} corresponds to the tree radius at DBH at the end of year $t-1$. Since all samples were taken near ground level, I used existing species-specific allometric equations to model DBH from inside-bark diameter at sample height for each calendar year (Omule and Kozak 1989). Modeled DBH values for individual trees were rescaled to ensure the estimated diameter outside the bark at 1.3 m matched the DBH measured at the time of sampling. Using the annual ring-width series, DBH and BAI series were calculated for all trees ($DBH \geq 1$ cm) for all calendar years over their lifespan.

4.2.4 Stand structure, composition, and stage of stand development

Contemporary structural attributes of tree density, basal area (BA; $m^2 ha^{-1}$), and quadratic mean diameter (QMD; $cm ha^{-1}$) were summarized for all trees, live trees only, and live trees by species in each stand. Stand-level density was summarized for each height class. These stand-level structural attributes were reconstructed back through time to assess stand development, as follows. Stand density was reconstructed using years of establishment (i.e., increases) and outer-ring dates of dead trees (i.e., decreases) to reconstruct changes in sampled populations. The DBH series from each tree was used to calculate BA and QMD for each stand through time. Stand-level BA was calculated for each calendar year as:

$$BA = \sum_i^n \left[k * \pi * \left(\frac{DBH_i}{200} \right)^2 \right] \quad (2)$$

where i represents the i th sampled tree in plots, n is the total number of sampled trees in plots, k

is a scaling factor to convert individual values to 1-ha equivalents, and DBH is diameter at breast height of each tree in cm. The scaling factor k was equal to 1 for canopy dominant trees, but varied for trees in subplots, depending on the distance of the furthest sampled tree in each DBH size class from plot center.

Stand-level QMD was calculated for each calendar year as:

$$QMD = \sqrt{\frac{BA}{0.0000785 * n}} \quad (3)$$

where BA is stand basal area in $m^2 ha^{-1}$, and n is the number of trees contributing to stand BA.

The stage of development was assessed by plotting the log-log relationship of stand density and QMD over time. For each stand, plots began the year that the maximum density of live trees (e.g., the onset of stem exclusion) was achieved and ended in 2012, the last full year of growth prior to sampling. Stands that exhibited increases in QMD while maintaining a constant density of live trees were undergoing stem exclusion. Stands that exhibited increases in QMD with simultaneous decreases in live tree density were undergoing stem exclusion and self-thinning. Plot trajectories were visually compared against a line with a slope of $-3/2$ as confirmation that stands were self-thinning. The earliest onset of stem exclusion among stands was 1928, which defined the time period (i.e., 1928 to 2012) for all subsequent analyses and reconstructions.

4.2.5 Indicators of stress among height classes and species

Tree ages and three indicators of stress (i.e., BAI growth rates, missing rings, and mortality) were summarized by height class and species. BAI growth rates and the percent of missing rings were calculated for each tree in two ways: (1) averaged over its lifespan; and (2) averaged over the stem-exclusion period. Tree ages, growth, and indicators of stress were quantified separately for live and dead trees to identify age-, vigour-, height class-, or species-

related factors associated with mortality.

For the period from 1928 to 2012 (i.e., the stem exclusion period), I assessed the temporal variations in growth patterns, the percentage of trees with missing rings, and the percentage of dead trees over time for (1) each height class (all species combined) and (2) only the canopy-dominant trees stratified by species. I developed two BAI chronologies for each height class and canopy-dominant species, using the R package *dplR* (Bunn 2008, 2010; Bunn *et al.* 2020; R Core Team 2019). Chronologies were developed by averaging the raw BAI values for each calendar year (i.e., raw mean chronology) and standardizing individual series with a horizontal line through the mean then averaging values for each calendar year to create unitless BAI indices (i.e., standard chronology). Temporal variations in growth patterns were assessed by testing for significant changes in slopes of standard BAI chronologies using the R package *segmented* (Muggeo 2003, 2008). This procedure iteratively fits a piecewise linear regression model to detect broken-line relationships in the slopes of each chronology, then calculates the slopes of the broken-lines (i.e., segments) and the points at which the slopes change (i.e., breakpoints; Muggeo 2003, 2008). Model parameterization requires initial estimation of the number and location of breakpoints; however, *segmented* implements a bootstrap restarting algorithm to ensure breakpoint estimates are robust to starting parameters. I identified a minimum of two and a maximum of four breakpoints among all chronologies. Models were parameterized using up to 5,000 iterations and the default tolerance. Segment breakpoints and slopes were compared among height classes and canopy-dominant species to determine when and how growth rates changed.

The percentages of trees with missing rings and dead trees were calculated for each height class and canopy-dominant species as the ratio of affected trees to the number of live trees

present in each year. These percentages were visually assessed by plotting their frequency over time and identifying (a) the height classes or canopy-dominant species with the greatest percentages of missing rings and tree deaths, and (b) how missing rings and tree deaths related to variations in BAI growth patterns.

4.2.6 Potential drivers and thresholds of stress in canopy dominant trees

To assess if climatic variation was associated with changes in growth rates of canopy-dominant trees, climate variables of monthly total precipitation (PPT), climatic moisture deficit (CMD) and minimum and maximum monthly temperature for the 20 study sites were obtained from ClimateNA (Wang *et al.* 2016). ClimateNA calculates CMD as the difference between Hargreaves reference evaporation and PPT (Wang *et al.* 2016). Climate records were averaged across all sites for each month and year to capture the dominant climate signal for the study area. Temporal variations in each climate variable were assessed by testing for significant changes in slopes between 1928 and 2012 using the R package *segmented* (Muggeo 2003, 2008), as described for the BAI chronologies. Breakpoints and slopes for the climate variables were compared with those for the BAI chronologies.

To assess if stand development was associated with changes in growth of canopy-dominant trees, I assessed potential relationships between growth patterns of canopy-dominant trees with the distribution of growing space among trees in different height classes. For each species (i.e., Douglas-fir, ponderosa pine and western larch), I identified the stands in which it was present in the canopy-dominant stratum, then extracted and averaged the percentages of basal area for living trees in each height class through time. Trends in the distribution of growing space among height classes were assessed for each canopy-dominant species. Thresholds of stress were inferred by comparing departures from the long-term average or breakpoints in the

BAI chronologies of each canopy-dominant species against changes in the relative basal area among height classes.

To assess potential drivers of missing rings and mortality among canopy-dominant trees of different species, I modelled linear relationships of the percent of missing rings and dead trees with (a) annual climate variables and (b) the additive form of the stand density index (ASDI), as formulated for mixed-age stands by Long and Daniel (1990). ASDI values were reconstructed for each year as:

$$ASDI = \sum_i N_i \left(\frac{DBH_i}{25} \right)^{1.6} \quad (4)$$

where N_i is the number of live and dead trees per hectare in the i th diameter class, and DBH_i is the diameter of the class. ASDI was calculated using midpoints of 5 cm diameter classes for each canopy dominant tree species and summarized for each stand for each year. Similarly, precipitation and CMD were binned in 50-mm classes, maximum temperature in 1-degree classes and minimum temperature in 2-degree classes. The percentages of missing rings and dead trees were averaged across bins for each climate variable and ASDI. For climate analyses, linear relationships were tested for significance ($\alpha = 0.05$) with the SAS REG Procedure (SAS Institute 2018). For ASDI analyses, non-linear relationships were tested for significance ($\alpha = 0.05$) with the SAS NLIN Procedure (SAS Institute 2018). Among significant climate variables and ASDI, thresholds of stress were defined as the value when $\geq 5\%$ of trees were missing a ring or dead.

4.3 Results

4.3.1 Stand Structure, Composition and Stage of Development

Stands contained 1,050 to 18,774 live and dead trees per hectare and, within stands, density decreased with increasing height class (**Table 4.1**). On average $24 \pm 16\%$ of trees (mean ± 1 SD) in stands were dead, ranging from $31 \pm 19\%$ of suppressed trees to $9 \pm 14\%$ of dominant

trees. However, only 1% of intermediate and co-dominant trees were dead; mortality in these two height classes occurred only in the densest stand (IDFX03). Stands averaged $31.7 \pm 8.2 \text{ m}^2 \text{ ha}^{-1}$ of basal area of live and dead trees, $5.4 \pm 3.7\%$ of which were dead. Stand QMD averaged 12.3 ± 3.2 cm for all live and dead trees, and 13.8 ± 3.5 cm for live trees only.

Trees were predominantly Douglas-fir (87%), followed by western larch (7%) and ponderosa pine (6%) (**Table 4.2**). Canopy dominant trees were primarily Douglas-fir (59%), with similar percentages of ponderosa pine (21%) and western larch (20%). Two, 6 and 26% of Douglas-fir, ponderosa pine and western larch canopy dominant trees, respectively, were dead. Lodgepole pine and Rocky Mountain juniper comprised only 0.4% of trees and were excluded from subsequent analyses given small sample sizes.

All stands were undergoing stem exclusion (**Fig. 4.1**). The first stand (IDFX02) began stem exclusion in 1928, and the final stand (IDFX04) began stem-exclusion in 2000 (**Table 4.1**). Additionally, all but three stands were undergoing self-thinning. Although trees died in stands PPX09, IDFX04 and IDFX12 during stem-exclusion, the rate of self-thinning did not approach a slope of $-3/2$ (**Fig 4.1**).

Tree ages increased with height class; canopy dominant trees were the oldest (183 ± 84 years) and suppressed trees the youngest (84 ± 23 years) (**Table 4.2**). Live co-dominant, intermediate, and suppressed trees were older than their dead counterparts. However, dead canopy dominant Douglas-fir and ponderosa pine averaged 94 ± 117 and 67 ± 148 years older than their living counterparts, respectively. Conversely, dead canopy dominant western larch were an average of 76 ± 155 years younger than their living counterparts.

Over their lifespans and during stem-exclusion, live trees in each height class had higher BAI growth rates than their dead counterparts (**Table 4.2**). As expected, nearly all dead trees had

lower BAI growth during stem-exclusion than over their lifespans. Interestingly, all living Douglas-fir and ponderosa pine trees had higher BAI growth during stem-exclusion, whereas live western larch had lower BAI growth.

In general, the percentage of missing rings was higher in live relative to dead trees, which was unexpected. As expected, missing rings were more common during stem exclusion than over the full lifespan of trees (**Table 4.2**). However, dead canopy-dominant Douglas-fir and ponderosa pine had more missing rings than their live counterparts. Overall, ponderosa pine had the highest percentages of missing rings, particularly during stem-exclusion. All dead canopy-dominant trees had higher percentages of missing rings during stem-exclusion than their live counterparts.

4.3.2 Indicators of Stress Among Height Classes

BAI growth rates increased with increasing height class and varied through time in all height classes (**Fig. 4.2a and b, Table 4.3a**). Initially growth rates decreased abruptly, then increased after 1931 although BAI was below the long-term average for all height classes. Tree growth in all height classes increased thereafter; growth rates of trees in lower canopy positions increased more than trees in the upper canopy. Growth declined again beginning in 1942 for suppressed and intermediate trees and in 1962 and 1966 for co-dominant and canopy-dominant trees, respectively. Rates of decline were highest for canopy-dominant trees, followed by suppressed, intermediate then co-dominant trees. The growth of suppressed, intermediate and co-dominant trees did not recover and decreased below the long-term average in 1978, 1993 and 2007, respectively. The growth of canopy-dominant trees increased since 1987, but has remained below the long-term average since 1977.

Percentages of trees with missing rings have generally increased over time, particularly

as growth rates decreased below the long-term average of suppressed and intermediate trees (**Fig. 4.2c**). Trees in the suppressed height class had the most missing rings, followed by intermediate and dominant trees, while co-dominant trees had the least.

Trees died between 1953 and 2012 (**Fig. 4.2d**). As expected, annual mortality was greatest among suppressed than intermediate trees; however, these were followed by dominant trees, which was not expected. Among canopy-dominant trees, deaths began in 1978, concurrent with growth rates decreasing below the long-term average. Thereafter, canopy-dominant tree death occurred in 15 additional years; one mode approached 2% mortality in 2001. Suppressed trees began dying in 1953 and mortality increased after growth rates decreased below the long-term average. Annual mortality was episodic with five modes exceeding 2% in 1975, 1988, 1991, 1995-6 and 2001-2. A maximum of 8% of intermediate and 6% of co-dominant trees died in 1983 and 1997, respectively, which exceeded the maximum annual mortality rate of canopy dominants. However, mortality among trees in intermediate and co-dominant height classes occurred only in the densest stand (IDFX03); the high percentages reflect the much higher numbers of intermediate and co-dominant trees in this stand relative to other stands.

4.3.3 Indicators of Stress Among Species

Average BAI growth rates were greater for Douglas-fir and ponderosa pine than western larch, but all varied through time (**Fig. 4.3a and b, Table 4.3b**). Initially growth rates decreased abruptly; western larch growth declined the most, followed by Douglas-fir and ponderosa pine. The growth rate of all species increased until 1942 to 1945; western larch had the greatest increase, followed by Douglas-fir and ponderosa pine. The growth trends of all species diverged thereafter. Douglas-fir growth slightly increased from 1942 to 1968, but decreased from 1968 to 1986. Growth was below the long-term average after 1978. From 1945 to 1982 ponderosa pine

growth decreased slightly, then decreased sharply from 1982 to 1987. From 1943 to 1987, western larch growth decreased consistently and decreased below the long-term average after 1969. After 1986–7, the growth rates of all species increased; ponderosa pine had the greatest increase, followed by Douglas-fir and western larch. The growth of ponderosa pine and Douglas-fir recovered to above their long-term averages in 2007 and 2008, respectively, but western larch growth remained below-average through 2012.

Rings were missing from all three species, with more missing from ponderosa pine and western larch than Douglas-fir (**Fig. 4.3c**). Rings were missed in Douglas-fir after growth rates decreased below the long-term average growth rate in 1968. Ponderosa pine began missing rings in 1949, much earlier than the other species, and had the most consistent accumulation of missing rings over time. Western larch began missing rings in 1973, after its growth rates decrease below the long-term average. Missing rings were episodic with five modes exceeding 10% in 1984, 1987, 2001, 2003 and 2009–10.

Canopy-dominant trees died from 1978 to 2008 (**Fig. 4.3d**). Few Douglas-fir or ponderosa pine dominant trees died. Mortality was greatest for western larch, with a strong mode in 2001–2, concurrent with many missing rings. For all species, mortality occurred when growth rates were below their long-term averages.

4.3.4 Drivers and Thresholds of Stress in Canopy-Dominant Trees

All four climatic variables had one significant breakpoint between 1928 and 2012 (**Table 4.3c, Fig. 4**). Minimum annual temperature, indicating winter conditions, increased slightly until 1984, then it increased faster. Similarly, maximum annual temperature, indicating summer conditions, decreased slightly until 1994, then it increased but at a lower rate than minimum temperature. Among the climatic variables, precipitation increased fastest until 1952, then it

decreased gradually. CMD decreased moderately until 1955, then decreased only slightly. Of these changes, only the minimum temperature breakpoint in 1984 coincided with increased growth of canopy-dominant trees after 1987 (**Table 4.3a**), with species-specific increases in Douglas-fir, ponderosa pine and western larch after 1986, 1986 and 1987, respectively (**Table 4.3b**).

The proportion of basal area occupied by trees in different height classes varied over time, with canopy-dominant trees continually occupying smaller proportions between 1928 and 2012 (**Fig. 4.5**). Co-dominant trees also occupied smaller proportions but reached minimums in basal area in 1998, 2001 and 2002 in stands occupied by Douglas-fir, ponderosa pine, and western larch, respectively. Conversely, intermediate trees consistently occupied greater proportions of basal area. Suppressed trees increased in proportion more quickly than intermediate trees, but reached maximums of 32% in 1984, 29% in 1984 and 35% in 1985, in stands occupied by Douglas-fir, ponderosa pine and western larch, respectively. The decline in proportion of basal area occupied by suppressed trees corresponded with increased mortality of trees in that height class. By 2012, the proportion of basal area occupied by suppressed trees decreased below that of intermediate trees in stands occupied by Douglas-fir and both intermediate and co-dominant trees in stands occupied by ponderosa pine. In contrast, suppressed trees still occupied the greatest proportion of basal area in stands occupied by western larch.

The final breakpoints in BAI, followed by increasing growth of Douglas-fir, ponderosa pine and western larch canopy-dominant trees, occurred exactly two years after the proportions of basal area occupied by suppressed trees began to decline (**Fig. 4.5**). Basal area of c. 28% occupied by suppressed trees consistently indicated a threshold. For Douglas-fir and ponderosa pine canopy-dominant trees, growth rates decreased and were below the long-term average when

the basal area occupied by suppressed trees was $>28\%$. Conversely, when mortality of suppressed trees caused the basal area to decrease to $\leq 28\%$ in 2007–8, growth rates of canopy-dominant trees increased and exceeded their long-term averages. Western larch growth rates decreased when the basal area of suppressed trees was only 9%. However, growth rates decreased and remained below the long-term average when basal area of suppressed trees increased to $\geq 28\%$, which persisted through 2012.

The percent of trees with missing rings and mortality generally increased with decreasing precipitation and increasing temperatures; however, few relationships with climatic variables were statistically significant (**Fig. 4.6**). For missing rings in Douglas-fir, only the linear increase with minimum temperature was significant (F-test = 13.58, $P = 0.006$); however, $< 1\%$ of trees missed rings at any given temperature. Similarly, for western larch only minimum temperature was significant (F-test = 12.4, $P = 0.008$). In years when minimum temperature was warmer than -10°C , up to 6% of western larch missed rings. For tree mortality, linear increases with minimum or maximum temperature were significant for all three species (Douglas-fir: F-test = 20.94, $P = 0.002$ and F-test = 10.64, $P = 0.01$; ponderosa pine: F-test_{Min. Temp.} = 41.21, $P_{\text{Min. Temp.}} = 0.0002$; western larch: F-test = 65.88, $P < 0.0001$ and F-test = 5.85, $P = 0.046$). For each 2°C increase in minimum or maximum temperature, mortality increased at rates of 0.08% and 0.2% for Douglas-fir, 0.4% _{Min. Temp.} for ponderosa pine, and 1.7% and 2.1% for western larch. However, $< 1.1\%$ of Douglas-fir and $< 3.1\%$ of ponderosa pine died at any given temperature. For western larch, up to 13.8% of trees died in years when minimum temperature was warmer than -14°C . It is notable that minimum temperature was only below -14°C in two out of the 28 years since 1984, but was below -14°C in 10 of the 28 years prior to and including 1984. No threshold for maximum temperature was detected since mortality of western larch was up to 19.1% across the observed

temperature range of 22 to 32°C.

The percent of trees with missing rings and mortality exhibited significant increasing, non-linear relationships with ASDI for Douglas-fir (F-test = 3815.76, $P < 0.0001$, and F-test = 2877.66, $P < 0.0001$, respectively), ponderosa pine (F-test = 227.13, $P < 0.0001$, and F-test = 690.07, $P < 0.0001$, respectively) and western larch (F-test = 19.27, $P = 0.0009$, and F-test = 33.20, $P = 0.0001$, respectively) (**Fig. 4.7**). Rings were missed in <3% of ponderosa pine and <4% of western larch until ASDI exceeded 700–800. At ASDI >700, the percent missing rings increased more rapidly in western larch than ponderosa pine. Rings were missed in <1% of Douglas-fir, until ASDI exceeded 1100. Western larch mortality was most sensitive to ASDI, with >5% of trees dying when ASDI exceeded 600. Mortality of ponderosa pine was $\leq 2\%$ of trees until ASDI exceeded 1000. Douglas-fir mortality was <1% of trees until ASDI exceeded 1100. The percent of dead trees increased non-linearly for each species when these ASDI threshold were exceeded. Overall, western larch mortality rates increased more rapidly than the accumulation of missing rings, while ponderosa pine and Douglas-fir were more prone to missing rings than mortality at the same ASDI levels.

4.4 Discussion

In high-density stands of southeastern BC, dendrochronological reconstructions showed canopy-dominant trees exhibited greater stress than trees in co-dominant and intermediate positions. In all species, this stress progressed in a sequence, causing growth decline, missing rings, then death. Indicators of stress escalated over time, triggered when stand-level relative BA of suppressed trees and ASDI exceeded thresholds, indicating competition rather than climate was the primary driver. Stress was greatest for western larch, followed by ponderosa pine, and least in Douglas-fir. The magnitude and timing of stress varied among species, related to species-

specific life history attributes affecting the ability to compete for below-ground resources. Next, I explain these findings in deeper detail and discuss the mechanisms by which sub-dominant trees can outcompete canopy-dominant trees for below-ground resources.

4.4.1 Stress in canopy-dominant trees

An unexpectedly high percentage of canopy-dominant trees exhibited multiple indicators of stress, and proportionally more dominant trees were stressed than trees in co-dominant and intermediate positions. Typically, stands self-thin during the stem-exclusion stage of development, when large trees outcompete smaller-statured trees for light, water, and other resources (Oliver and Larson 1996). This asymmetrical, size-based competition drives disproportionate mortality of small trees (Oliver and Larson 1996, Schwinning and Weiner 1998), allowing survivors to accumulate greater biomass. Consistent with expectations, I found that trees in the suppressed canopy position were most abundant, smallest in diameter, and had the greatest degree of absolute and proportional stress. Moreover, Douglas-fir was most common in the suppressed and intermediate positions, owing to its relative shade tolerance. There were few ponderosa pine and even fewer western larch in these subcanopy positions since both species are shade intolerant. However, my study stands became highly unproductive, maintaining 864-14,053 live trees per hectare, despite subcanopies establishing 82-145 years ago (Chapter 2). Although most stands have self-thinned, annual rates of change were exceptionally slow given the high densities and age of subcanopy trees. Consequently, trees across all size classes showed multiple signs of stress, including canopy-dominant trees.

During stand development, the BAI of canopy-dominant trees is expected to increase, asymptote during the juvenile growth period, then maintain a relatively constant level once trees mature (Biondi and Qeadan 2008). The BAI of canopy-dominant trees should not decline unless

trees become senescent, have been disturbed or they are stressed. Thus, it is concerning that the BAI growth of canopy-dominant trees declined and they began to miss rings, regardless of species. Once growth rates decreased below long-term averages, these trees missed even more rings and began to die.

Declining BAI and other indicators of stress were not driven by senescence. While dead Douglas-fir and ponderosa pine trees averaged 262 years of age and were 90 years older than their living counterparts, tree ring reconstructions indicated large trees of these species regularly lived longer than 400 years in the past. Additionally, most Douglas-fir and ponderosa pine canopy-dominant trees (98% and 94%, respectively) were alive and young (averaging 172 years of age). Despite their youth, both species had reduced growth rates and missing rings, indicating alternate factors must explain the decreased growth of these trees. In contrast to Douglas-fir and ponderosa pine, dead western larch averaged 169 years of age and were 76 years younger than their living counterparts, which does not identify age as a driver of western larch mortality. Tree-ring reconstructions also showed that large western larch regularly lived more than 400 years in the past. None of these trends identify senescence as a reason for decreased growth, or explain the other indicators of stress.

Since BAI growth decline was exhibited at the population level in all species and over long periods, it was unlikely to be driven by discrete disturbances or weather events, such as insect outbreaks and droughts. Instead, the inverse relationship between the growth rate and occurrences of missing rings and tree death is consistent with other research on stressed trees (Lorimer *et al.* 1999, Bigler *et al.* 2004, Novak *et al.* 2016a). In my study, the progression of stress in canopy-dominant trees was corroborated by multiple lines of evidence. BAI declined before other signs of stress were evident. Live trees had higher percentages of missing rings

during the stem-exclusion stage than over their lifespans, while trees that died had more missing rings than survivors. Missing rings and mortality of canopy-dominant trees increased with stand density and BA, represented by ASDI.

4.4.2 How are sub-dominant trees outcompeting canopy dominant trees?

Inverse asymmetrical competition, in which dense subcanopy trees outcompete canopy trees (Biondi 1996), is consistent with stand structures and indicators of tree stress in various canopy strata. In the absence of self-thinning, inter-tree competition for resources inevitably intensified through time within stands. Stress in canopy-dominant trees (relative to lower canopy strata) suggest competition for below-ground resources (i.e., water, nutrients, space), since small trees cannot outcompete canopy-dominant trees for above-ground resources (i.e., light, growing space) (Oliver and Larson 1996). Intense below-ground competition is also consistent with the dry regional climate of the study area, where soil moisture strongly limits tree growth.

Large trees inadvertently contribute to the persistence of high densities of small trees through hydraulic redistribution, at their own expense. At moisture-limited sites, root growing space is maximized before crowns close (Oliver and Larson 1996). Numerous studies have shown absolute root depth and size of root systems decrease with increasing aridity and stand density (Schulze *et al.* 1996, Schenk and Jackson 2002). At the same time, relative root size and depth increase proportional to tree size (McMinn 1962, Hodgkins and Nichols 1977, Mauer and Palatova 2012). Therefore, on densely stocked sites, greater than 90% of root biomass is concentrated close to the soil surface (e.g., above 0.60 m; Schulze *et al.* 1996). Consequently, small trees with shallow roots depend on limited precipitation that penetrates upper soil layers, while large trees access deep soil moisture reserves (Kerhoulas *et al.* 2013a). However, small trees benefit from hydraulic redistribution, or the passive transport of soil water via roots from

deep moist soils to upper dry horizons (Neumann and Cardon 2012). For example, in a loblolly pine (*Pinus taeda* L.) plantation, shallow-rooted subcanopy trees depended on water redistributed by deep-rooted canopy trees for their early summer water supply (Domec *et al.* 2010). A possible side effect of hydraulic redistribution in dense stands is that larger, deep-rooted trees inadvertently supply deep soil water to smaller, shallow-rooted trees at their own expense (Neumann and Cardon 2012).

Hydraulic redistribution varies among species and size of trees in two ways that are consistent with indicators of stress in my study area. Douglas-fir and ponderosa pine use hydraulic redistribution to prevent fine root embolism when soils dry (Domec *et al.* 2004). However, large, old trees are better at redistributing soil water than small, young trees, as are Douglas-fir over ponderosa pine. Douglas-fir may be usurping deep soil water, confounding stress in ponderosa pine and western larch canopy-dominant trees. Since rooting depth increases with tree height (McMinn 1962, Mauer and Palatova 2012), trees in different strata rely on different mechanisms to access soil moisture. Suppressed trees with shallow roots may uptake precipitation when it is available, but otherwise depend on hydraulic redistribution by canopy-dominant trees. Intermediate and co-dominant trees with deeper roots may access sub-surface soil moisture, but also benefit from hydraulic redistribution by canopy-dominant trees. In this scenario, canopy-dominant trees have a near constant demand for water from trees in all sub-dominant strata. In dense stands on moisture stressed sites, stress would be greatest on canopy-dominant and suppressed trees, as I observed in my study area.

Differences in the degrees of stress are consistent with other life history attributes that distinguish western larch, ponderosa pine, and Douglas-fir. Of the three species, canopy-dominant western larch exhibited the most stress. The deciduous nature of western larch sets it apart from

the other species, affecting its ability to tolerate drought. As a deciduous tree, western larch leaves senesce under severe stress (Silla and Escudero 2006, Marchin *et al.* 2010, Sparks *et al.* 2018), a beneficial strategy during short-term drought. However, the need to allocate carbon to grow a new complement of foliage annually is a trade-off with ring-formation that could be detrimental in consecutive years of drought, especially in dense stands where trees are always stressed from competition. Douglas-fir exhibited less stress than ponderosa pine, although ponderosa pine is more tolerant of heat and water deficits (Klinka *et al.* 2003). However, being shade-tolerant may benefit Douglas-fir in dense stands, while ponderosa pine is intolerant of low light and western larch requires exposure (Klinka *et al.* 2003).

Mycorrhizal networks and root grafting may benefit Douglas-fir sub-dominant trees at the expense of canopy dominant trees. Below ground, all three species form symbiotic relationships with mycorrhizal fungi that transport carbon, nutrients, and water among trees (Simard 2009; Beiler *et al.* 2009); although inter-species sharing of resources also occurs (Song *et al.* 2015). A beneficial attribute of Douglas-fir is root grafting (Lanner 1961), which was evident from the abundance of living stumps of this species in sampled stands. When the roots of two or more trees graft, surviving trees provide carbohydrates to stumps of cut trees, which generate new tissues (Bormann 1966). The percentage of trees with root grafts increases with stand density due to the closer proximity of trees (Fraser *et al.* 2005). In jack pine (*Pinus banksiana. L.*), trees with root grafts grow more than trees without root grafts (Tarroux and DesRochers 2011). Trees with better access to resources share them with trees growing on drier or poorer microsites, and subcanopy trees benefit from large canopy trees (Tarroux and DesRochers 2011). Root grafts allow subcanopy trees to survive when they would otherwise die from suppression (Oliver and Larson 1996), but can be costly to large trees in dense stands.

4.4.3 Stress is driven by competition more than climate

My reconstructions of stand development through time provide strong evidence that competition primarily drives stress. Signs of stress in canopy-dominant trees were triggered when stands crossed critical thresholds of BA and ASDI. The relative BA of suppressed trees influenced the growth decline, recovery, and rate of recovery of canopy-dominant trees. When suppressed trees exceeded 28% of stand basal area, Douglas-fir, ponderosa pine, and western larch exhibited clear declines in growth. Conversely, two years after the declines in the relative basal area of the suppressed trees, canopy-dominant trees of all three species switched back to increasing growth. As the relative basal area of suppressed trees decreased toward 28%, the rate of recovery of canopy-dominant trees increased.

Missing rings and mortality of canopy-dominant trees increased with increasing ASDI and appeared to exhibit species-specific thresholds. ASDI is a measure of stand density and the area occupied by trees. A single large-diameter tree has a greater impact on ASDI than a small-diameter tree; yet, abundant small-diameter trees can generate much larger ASDI values than a few large trees. In my study, stress in canopy-dominant trees was strongly tied to the abundance of trees in sub-dominant positions. Suppressed and intermediate trees comprised over 60% of average annual ASDI since 1928, and suppressed trees comprised the greatest proportion of ASDI since 1946. After 1946, when ASDI exceeded species-specific thresholds, missing rings and tree mortality increased. Western larch exhibited the greatest stress, followed by ponderosa pine. Western larch is most likely to miss rings and is highly susceptible to mortality when ASDI exceeds 600. Mortality rates of ponderosa pine do not increase until ASDI exceeds 1000. Douglas-fir exhibited the least stress, with missing rings and mortality rates increasing only when ASDI exceeded 1100.

Discrepancies between long-term trends in climate and growth of canopy-dominant trees do not support climate as the primary driver of stress. Since moisture limits tree growth in the study area, I expected long-term changes in precipitation, temperature, and climatic moisture deficit to affect the growth trends of drought-sensitive western larch, ponderosa pine and Douglas-fir. However, the increased growth of canopy-dominant trees after 1984 is at odds with historical climate trends. Precipitation has decreased since 1952, climatic moisture deficits remained nearly constant since 1955, and minimum and maximum temperatures have increased since 1984 and 1994, respectively. These climate trends indicate an overall decrease in water availability, so the increases in tree growth after 1986 contrast expectations. Several studies have documented increases in long-term tree growth in response to increasing temperatures (Salzer *et al.* 2009, McMahon *et al.* 2010, Silva *et al.* 2016); however, they were at energy-limited sites (Stephenson 1990), where warmer temperatures enhance growth (Littell *et al.* 2008, Clark *et al.* 2016). In contrast, increasing temperatures at moisture-limited sites drive tree growth decline and death, unless accompanied by increasing moisture availability (Littell *et al.* 2008, van Mantgem *et al.* 2009, Hankin *et al.* 2019). Consequently, the increasing growth trends observed in this study appear to contrast historical climate trends.

Increasing minimum temperatures, which began in 1984, may indirectly explain the recovery of BAI growth rates in canopy-dominant trees. The increase in minimum temperature coincided with two important changes. First, the mortality of suppressed trees increased, thus their relative BA declined. Subsequently, the BAI of canopy-dominant trees increased after 1986. Second, warmer winters indirectly affect moisture availability during the growing season because less snow and earlier snow melt extend the growing season but also reduce soil moisture recharge, thus producing greater moisture deficits during summer drought (Loik *et al.* 2004). If

these indirect impacts on moisture availability contributed to high mortality of suppressed trees, then reduced competition for soil moisture could explain the increased growth rates of canopy-dominant trees.

4.5 Conclusions

Past management practices, including selective harvesting, fire suppression, and the prevention of Indigenous fire stewardship, have generated dense, unproductive stands throughout southeastern BC's dry forests. Trees in these stands are stressed: growth rates have declined, missing rings have increased, and many trees are dying. Canopy-dominant trees are more stressed than trees in the co-dominant and intermediate height classes, most likely caused by competition for soil moisture. Among species, western larch was most stressed, while Douglas-fir was least stressed, owing to differences in life history attributes. Mortality of suppressed trees since the 1980s has eased competition, allowing Douglas-fir and ponderosa pine canopy-dominant trees to recover to above-average growth rates. However, western larch remains highly stressed. In these stands, thinning treatments to remove subcanopy trees would alleviate competition and enhance the resilience of residual co-dominant and canopy dominant trees to fires and droughts. Dense stands containing western larch should be prioritized to ensure long-term persistence of this species in the study area.

4.6 Tables

Table 4.1 Stand density, basal area (BA) and quadratic mean diameter (QMD) for the 20 study plots.

Plots are arranged from lowest density (top) to highest density (bottom). Stem-Exclusion is the last year of tree establishment, and each stand reached the stem-exclusion stage of development.

Site	Density (% live)										BA (% live)		QMD		Stem-Exclusion
	Total		Height Class								(m ² ha ⁻¹)	(cm)			
			Suppressed		Intermediate		Co-dominant		Dominant			Total	Total	Live	
PPX02	1050	(82)	560	(68)	310	(100)	160	(100)	20	(82)	18.9	(92)	15.1	16.0	1991
IDFX12	1161	(100)	601	(100)	449	(100)	96	(100)	16	(93)	19.3	(99)	14.5	14.5	1976
PPX03	1325	(80)	902	(70)	170	(100)	218	(100)	35	(97)	31.8	(98)	17.5	19.4	1944
IDFX13	1460	(74)	1145	(67)	159	(100)	138	(100)	19	(100)	34.9	(97)	17.5	20.0	1977
IDFX04	1546	(95)	1375	(94)	100	(100)	50	(100)	21	(100)	19.0	(95)	12.5	12.5	2000
IDFX08	1848	(54)	1285	(34)	525	(100)	25	(100)	13	(100)	27.8	(88)	13.8	17.6	1941
IDFX09	1867	(87)	1444	(84)	270	(100)	116	(100)	37	(97)	25.9	(98)	13.3	14.1	1992
PPX07	2191	(75)	1546	(65)	513	(100)	104	(100)	28	(96)	29.4	(94)	13.1	14.7	1958
PPX08	2216	(90)	1635	(86)	420	(100)	130	(100)	31	(100)	41.4	(98)	15.4	16.1	1952
IDFX07	2485	(58)	2126	(51)	278	(100)	44	(100)	37	(97)	33.8	(95)	13.2	16.8	1982
IDFX14	2530	(73)	2238	(69)	143	(100)	125	(100)	25	(96)	29.6	(93)	12.2	13.8	1960
PPX10	2532	(92)	2141	(90)	294	(100)	75	(100)	22	(100)	34.7	(98)	13.2	13.7	1976
IDFX11	3344	(83)	2576	(78)	528	(100)	226	(100)	14	(92)	39.2	(97)	12.2	13.2	1960
IDFX10	3454	(71)	3278	(70)	102	(100)	50	(100)	24	(86)	23.6	(94)	9.3	10.7	1970
IDFX05	4003	(58)	2953	(43)	678	(100)	339	(100)	33	(82)	43.4	(93)	11.8	14.9	1960
PPX04	4345	(46)	3583	(35)	664	(100)	73	(100)	25	(100)	25.5	(89)	8.6	12.0	1946
IDFX02	4616	(83)	3053	(74)	1065	(100)	477	(100)	21	(100)	40.9	(97)	10.6	11.5	1928
IDFX06	6547	(51)	5735	(44)	674	(100)	101	(100)	37	(39)	43.9	(87)	9.2	12.1	1979
PPX09	6618	(92)	5712	(90)	686	(100)	208	(100)	13	(92)	27.6	(99)	7.3	7.6	1978
IDFX03	18774	(75)	14381	(73)	3857	(80)	521	(80)	15	(75)	40.6	(89)	5.3	5.7	1951

Table 4.2 Ages, growth rates and missing rings for the dominant tree species.

Metrics of sample depth (i.e., the number of samples used to derive metrics, scaled to per ha densities), average tree ages, average basal area increment (BAI), and the percentage of trees with missing rings are reported for live (L) and dead (D) trees in each canopy height class, including dominant (D), co-dominant (CD), intermediate (I) and suppressed (S). Lifespan includes all years when trees were alive, whereas stem-exclusion only includes years when stands were in the stem-exclusion stage of development.

Species	Ht Class	Sample Depth		Age		BAI (cm ²) (mean $\pm$ SD)				Missing Rings (%) (mean $\pm$ SD)			
		(scaled)		(mean $\pm$ SD)		Lifespan		Stem-exclusion		Lifespan		Stem-exclusion	
		L	(D)	L	(D)	L	(D)	L	(D)	L	(D)	L	(D)
Douglas-fir	D	281	(5)	162 $\pm$ 62.2	(255 $\pm$ 121.4)	11.2 $\pm$ 5.2	(8.2 $\pm$ 0.4)	12.3 $\pm$ 6.3	(4.4 $\pm$ 2.5)	0.1 $\pm$ 0.8	(0.4 $\pm$ 0.7)	0.4 $\pm$ 2.5	(2.9 $\pm$ 5)
	CD	2627	(102*)	122 $\pm$ 42.9	(69 $\pm$ 0)	6.7 $\pm$ 4.4	(1.6 $\pm$ 0)	7.7 $\pm$ 4.8	(1.9 $\pm$ 0)	0.1 $\pm$ 0.3	(0 $\pm$ 0)	0 $\pm$ 0.3	(0 $\pm$ 0)
	I	9565	(771)	98 $\pm$ 24.5	(90 $\pm$ 2.9)	2.9 $\pm$ 2.1	(0.5 $\pm$ 0.3)	3.2 $\pm$ 2.5	(0.7 $\pm$ 0.4)	1.1 $\pm$ 3.1	(0.9 $\pm$ 1.8)	2.3 $\pm$ 8.7	(1.5 $\pm$ 3)
	S	35111	(15713)	89 $\pm$ 21.6	(70 $\pm$ 18.8)	1.1 $\pm$ 1	(0.4 $\pm$ 0.5)	1.1 $\pm$ 1.1	(0.3 $\pm$ 0.5)	7.5 $\pm$ 10.7	(3.7 $\pm$ 5.8)	11.7 $\pm$ 16.6	(6.6 $\pm$ 11)
Ponderosa pine	D	97	(6)	201 $\pm$ 72.2	(268 $\pm$ 144.2)	9.6 $\pm$ 4.7	(3.2 $\pm$ 2.2)	12.9 $\pm$ 7.9	(2.1 $\pm$ 2.2)	0.6 $\pm$ 1.8	(3.5 $\pm$ 3.8)	2.3 $\pm$ 7.8	(14.2 $\pm$ 15.7)
	CD	311	(0)	177 $\pm$ 83.5	-	6.5 $\pm$ 4	-	6.6 $\pm$ 3.5	-	1.2 $\pm$ 2	-	3.2 $\pm$ 5.8	-
	I	811	(0)	101 $\pm$ 24.7	-	3.9 $\pm$ 2.3	-	4.6 $\pm$ 3	-	2 $\pm$ 4.4	-	4.2 $\pm$ 9.3	-
	S	2237	(793)	95 $\pm$ 23.8	(81 $\pm$ 24.4)	1 $\pm$ 0.8	(0.8 $\pm$ 0.8)	1 $\pm$ 1	(0.5 $\pm$ 0.4)	13.5 $\pm$ 13.8	(10.1 $\pm$ 12.3)	21.6 $\pm$ 27	(21.7 $\pm$ 29.4)
Western larch	D	72	(25)	245 $\pm$ 127.8	(169 $\pm$ 91.7)	6.2 $\pm$ 3.4	(5.1 $\pm$ 2.8)	5.8 $\pm$ 3.5	(2.4 $\pm$ 1.7)	1.1 $\pm$ 3.6	(0.9 $\pm$ 1.4)	3.9 $\pm$ 10.1	(4.3 $\pm$ 6.9)
	CD	225	(0)	180 $\pm$ 79.1	-	4.6 $\pm$ 2.7	-	3.8 $\pm$ 1.3	-	0 $\pm$ 0	-	0 $\pm$ 0	-
	I	726	(0)	89 $\pm$ 21.9	-	3.3 $\pm$ 2	-	2.9 $\pm$ 1.8	-	1.4 $\pm$ 3	-	2.4 $\pm$ 4.1	-
	S	2021	(2134)	84 $\pm$ 12	(65 $\pm$ 16.7)	1.6 $\pm$ 1	(0.6 $\pm$ 0.5)	1.4 $\pm$ 0.9	(0.5 $\pm$ 0.5)	3.4 $\pm$ 5.5	(3.1 $\pm$ 4.6)	5.1 $\pm$ 9.2	(3.7 $\pm$ 6.4)

* Metrics derived from a single tree; unable to calculate SD

Table 4.3 Segments, slopes and breakpoints detected in standardized basal area increment chronologies and climate variables with segmented regression analysis, from 1928-2012.

Breakpoints separate significantly different slopes ($\alpha=0.05$), indicating changes in (a) growth rates of trees in each canopy height class, (b) growth rates of each canopy dominant species, and (c) climate variables.

	Parameter	Segment 1		Segment 2		Segment 3		Segment 4		Segment 5
		Slope	Break	Slope	Break	Slope	Break	Slope	Break	Slope
(a)	Dominant	-0.2516	1931	0.0139	1966	-0.0223	1987	0.0081	-	-
	Co-dominant	-0.2715	1931	0.0141	1962	-0.0042	-	-	-	-
	Intermediate	-0.3969	1932	0.0592	1942	-0.0063	-	-	-	-
	Suppressed	-0.5441	1931	0.0868	1942	-0.0162	-	-	-	-
(b)	Douglas-fir	-0.1116	1936	0.0895	1942	0.0051	1968	-0.0182	1986	0.0072
	Ponderosa pine	-0.0341	1940	0.1623	1945	-0.00002	1982	-0.1230	1986	0.0142
	Western larch	-0.0633	1939	0.5375	1943	-0.0239	1987	0.0054	-	-
(c)	Min. temperature	0.0202	1984	0.1488	-	-	-	-	-	-
	Max. temperature	-0.0110	1994	0.0881	-	-	-	-	-	-
	Precipitation	5.5610	1952	-0.5884	-	-	-	-	-	-
	Climatic moisture deficit	-3.7881	1955	-0.0190	-	-	-	-	-	-

4.7 Figures

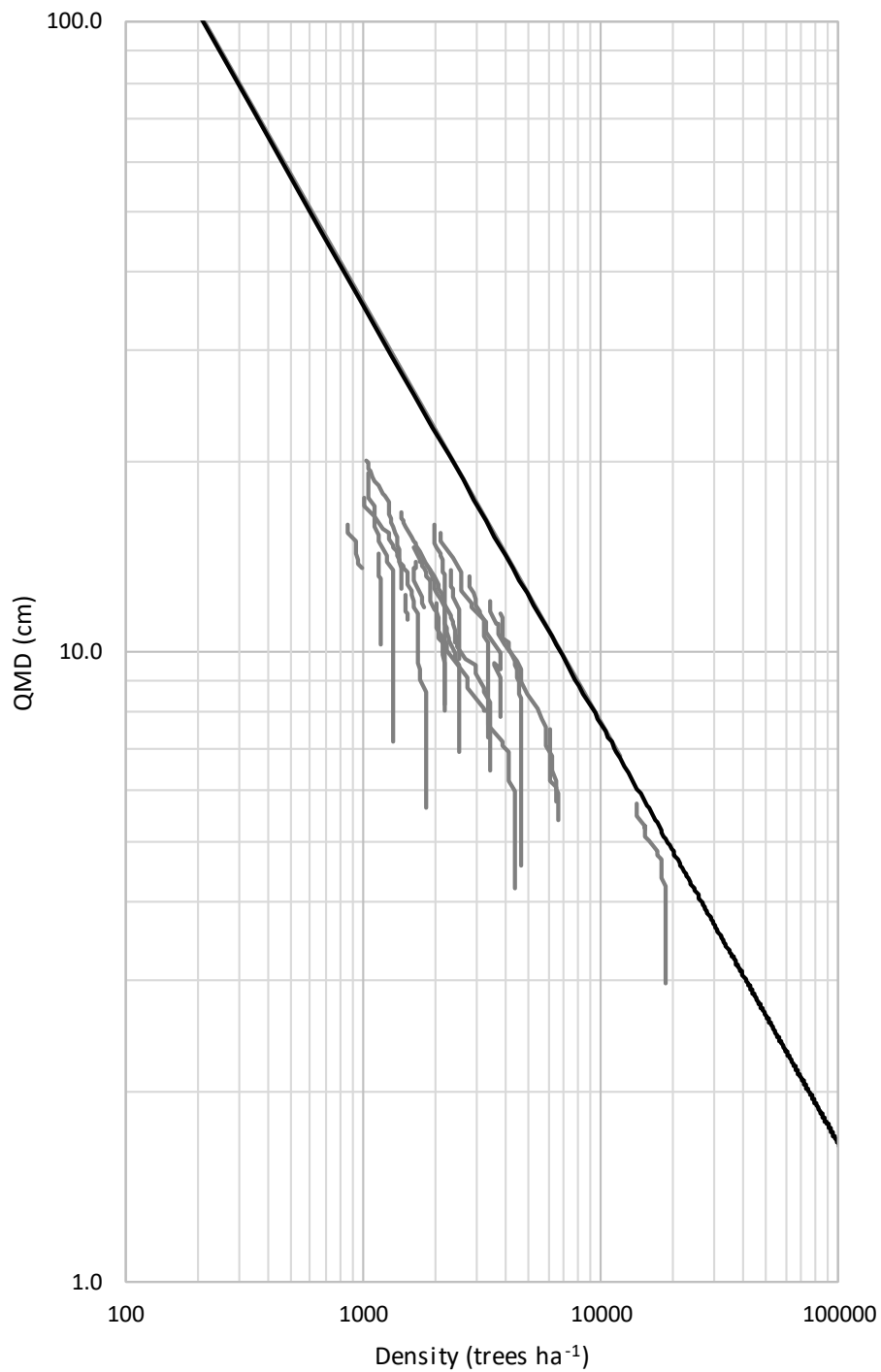


Figure 4.1 Assessment of self-thinning and stage of stand development.

Lines represent individual stands from the first year each stand reached maximum density of live trees to 2012. The diagonal black line with a slope of -1.5 represents the standard rate of self-thinning (Yoda *et al.* 1963).

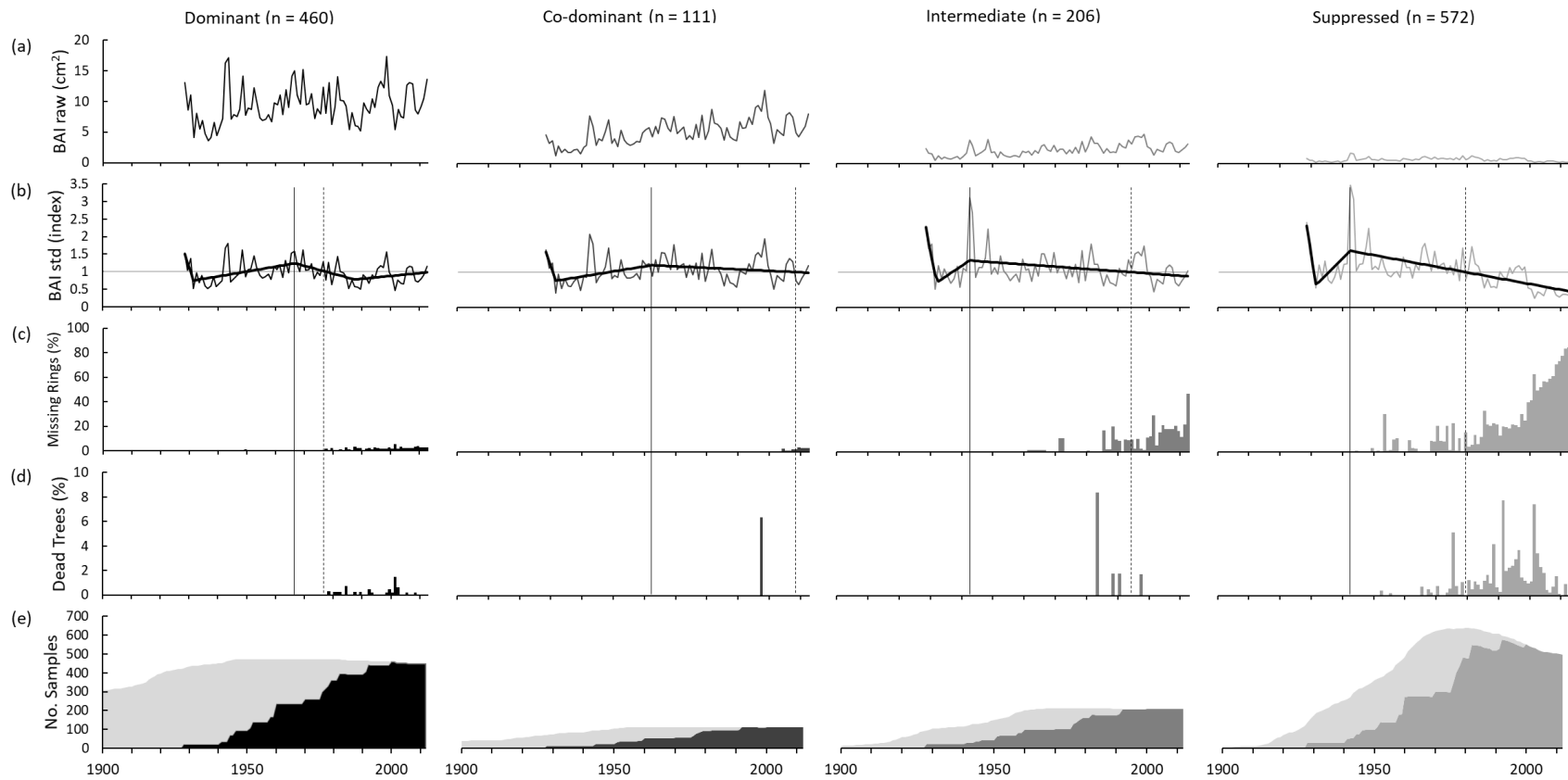


Figure 4.2 Indicators of stress among trees stratified by height class.

(a) Raw and (b) standardized basal area increments (BAI) show growth rates through time. Black lines overlaid on standard BAI curves indicate significant breakpoints; horizontal grey lines indicate the long-term average BAI. Percentage of (c) missing rings relative to the number of live trees per year and (d) trees deaths relative to the number of live and dead trees per year. (e) Sample depth curves show the number of trees alive per year over the lifespan of trees (light grey) and during the period of stem exclusion (dark grey). Vertical lines through panels b-d indicate the onset of long-term growth decline (solid) and years when growth decreased below long-term average (dashed) for each height class.

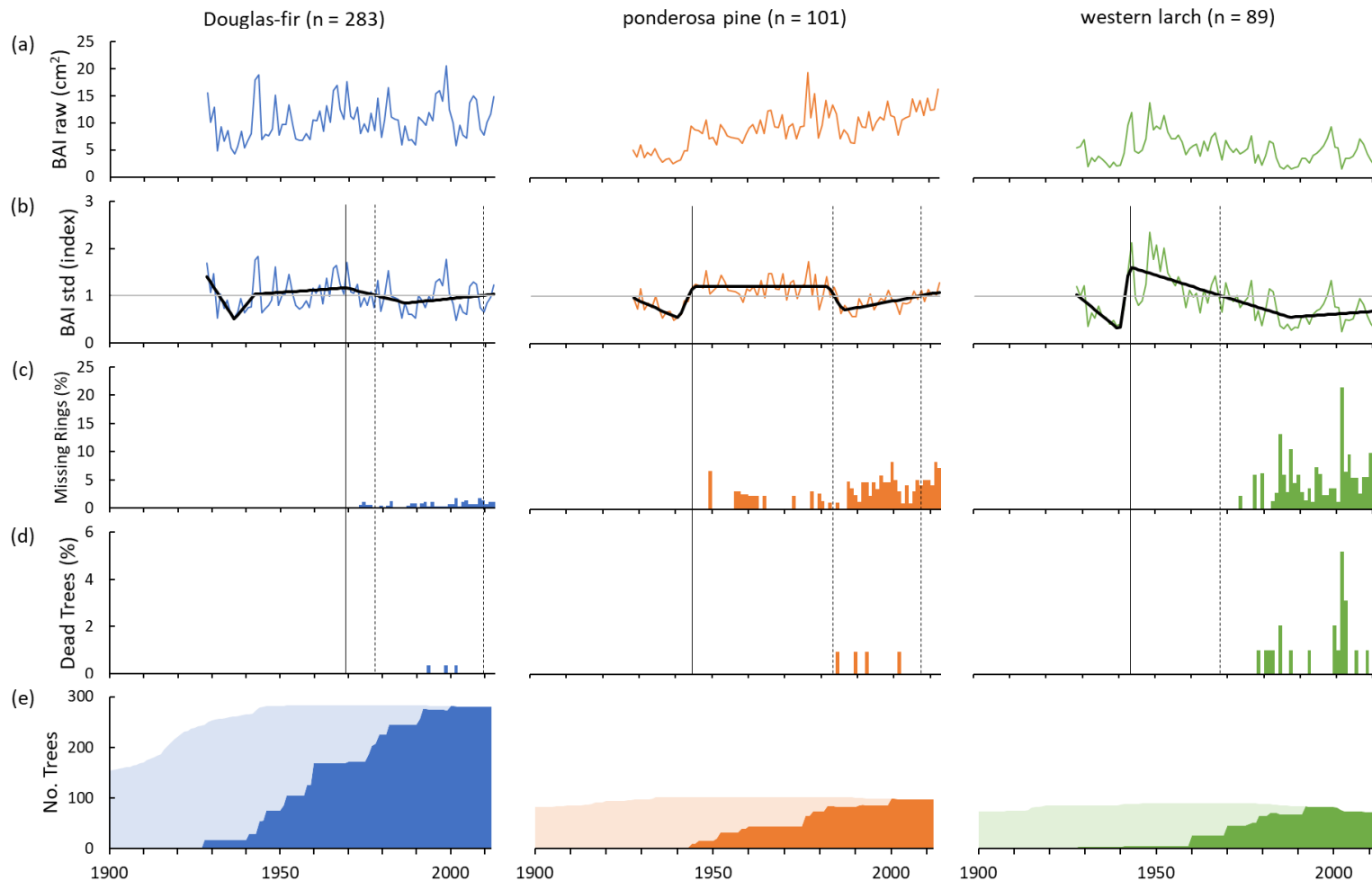


Figure 4.3 Indicators of stress among canopy-dominant trees stratified by species.

(a) Raw and (b) standardized basal area increments (BAI) show growth rates through time. Black lines overlaid on standard BAI curves indicate significant breakpoints; horizontal grey lines indicate the long-term average BAI. Percentage of (c) missing rings relative to the number of live trees per year and (d) trees deaths relative to the number of live and dead trees per year. (e) Sample depth curves show the number of trees alive per year over the lifespan of trees (light colours) and during the period of stem exclusion (dark colours). Vertical lines through panels b-d indicate the onset of long-term growth decline (solid) and years when growth decreased/increased relative to the long-term average (dashed) for each species.

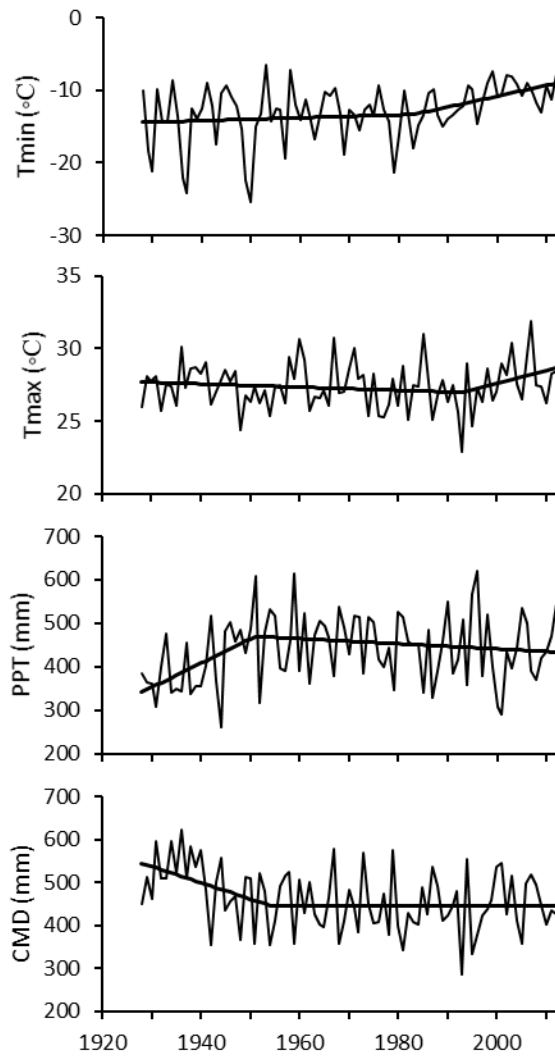


Figure 4.4 Climatic trends for the study area (1928–2012).

The climate variables include minimum temperature (Tmin), maximum temperature (Tmax), precipitation (PPT) and climatic moisture deficit (CMD). Black lines on annual climate data indicate significant breakpoints in the slopes of linear climate trends.

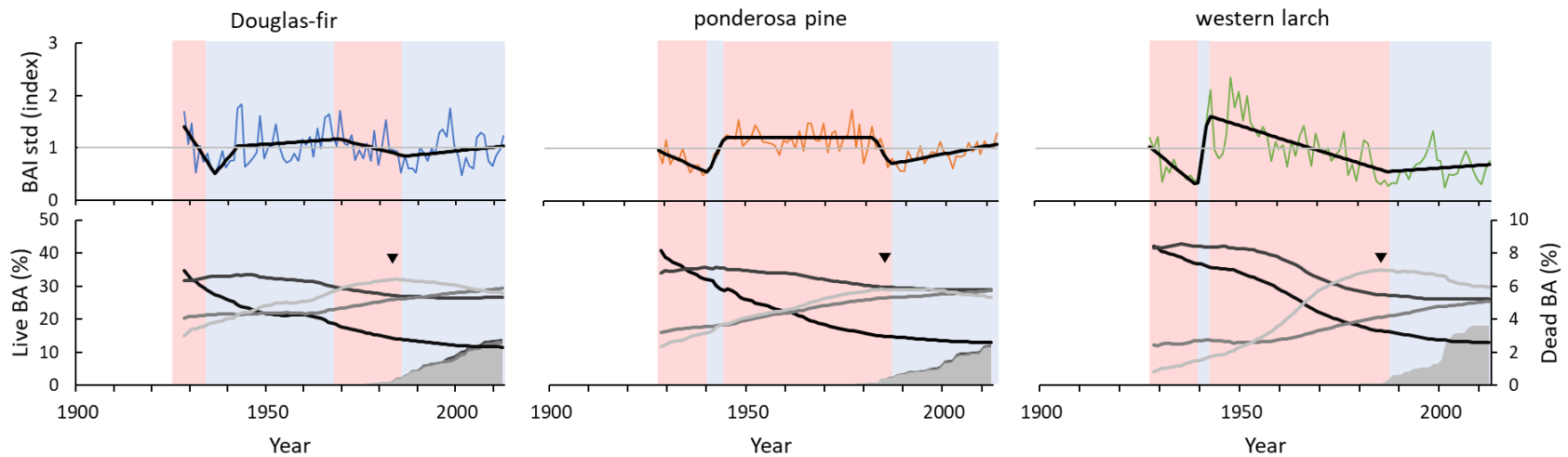


Figure 4.5 Species-specific growth rates of canopy-dominant trees relative to stand structure (1928-2012).

Top: For each species, black lines overlaid on standard BAI curves indicate significant breakpoints in growth trends and horizontal grey lines indicate the long-term average BAI. Periods with increasing/decreasing BAI trends are highlighted in blue/red. Vertical dashed lines indicate years when BAI trends cross the long-term average. Bottom: The relative basal area of living trees (lines) and dead trees (bars), stratified by height class (light grey = suppressed, medium grey = intermediate, dark grey = co-dominant, black = dominant). Black triangles indicate years with the maximum relative basal area of live trees in the suppressed height class.

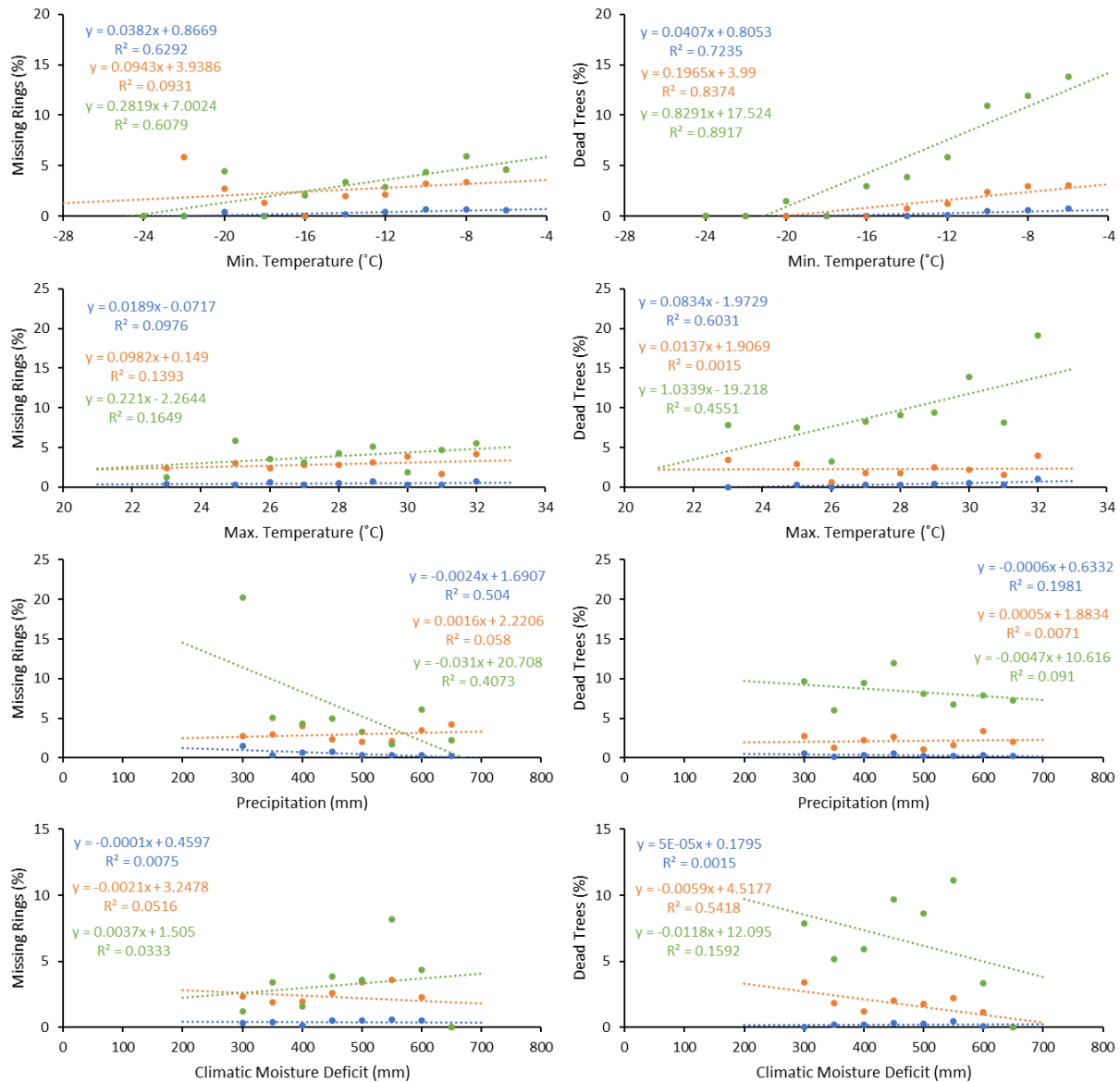


Figure 4.6 Relations between climate and indicators of stress among canopy-dominant trees by species.

For each climatic variable, dashed lines and equations depict linear trends in missing rings (left column) and tree deaths (right column) for Douglas-fir (blue), ponderosa pine (orange) and western larch (green).

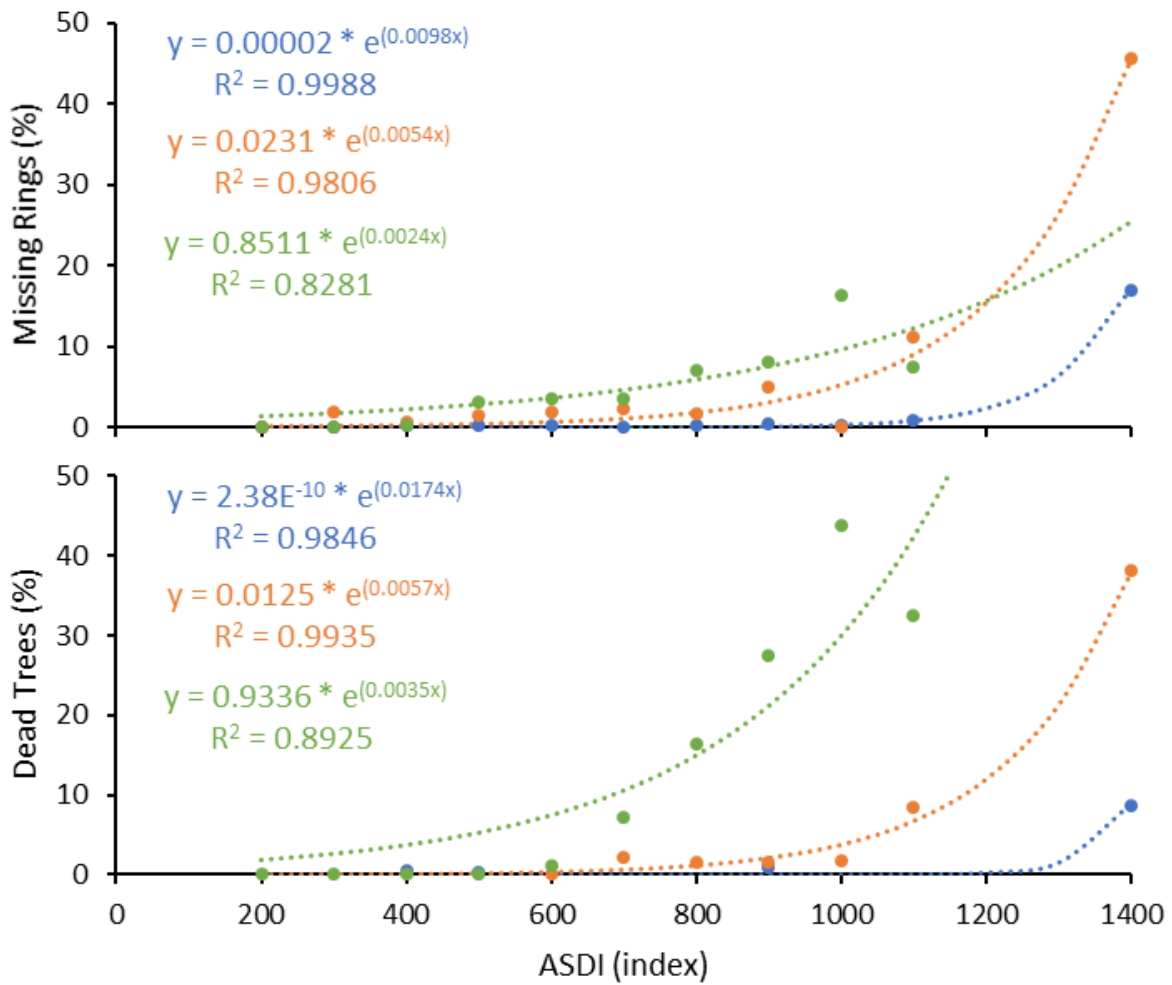


Figure 4.7 Indicators of stress relative to stand structure among canopy-dominant trees by species. Dashed lines depict non-linear trends in the missing rings (top) and tree deaths (bottom) by 100-unit Additive Stand Density Index (ASDI) classes for Douglas-fir (blue), ponderosa pine (orange) and western larch (green).

Chapter 5: Conclusion

5.1 Research contributions

Understanding the trajectory of dry forests and their resilience is critical to ensure their persistence in a rapidly warming climate. Warming global climate, with the associated increases in fire size and severity, along with our reactive but ineffective responses to catastrophic fires (Sankey 2019) suggest our contemporary management paradigms are not keeping pace.

Unfortunately, these dynamics can have dire consequences for dry forest ecosystems. In the interior of southern British Columbia, the enduring importance of dry forests social-ecological systems is abundantly clear. Situated in warm valley bottoms in proximity to many essential resources has meant dry forests are the most intensively inhabited and utilized ecosystem by both Indigenous people and European settlers. These same ecosystems are now home to the largest population centers in the interior, accounting for 16% of British Columbia's total population. Consequently, the influence of humans in these forests are profound; however, the degree to which humans have shaped and altered the resilience of these forests remained unclear prior to this study. Moreover, differing perspectives of historical fire regimes provided conflicting interpretations of ecosystem degradation and resilience that led some to question proactive management of dry forests aimed at altering their resilience trajectories.

The findings of my dissertation, which examined contemporary dense, dry forests in southeastern British Columbia, contribute to our understanding of historical dry forest fire regimes. Firstly, the research revealed how Indigenous use of fire shaped the historical lower-severity fire regime and shaped historical forest composition and structure. Second, the research showed how subsequent European "settler" forest management practices of fire exclusion and

selective harvesting interacted to impact these forests in three key ways: (a) altering the historical fire regime, (b) promoting highly dense stands, and (c) degrading the fire resilience of the dry forest matrix. By reconstructing historical fires, harvesting, and forest dynamics, my dissertation research provides baseline metrics for the historical range of variability (HRV) to determine where proactive management of dry forests is needed.

5.2 Summary and main findings

Reconstructions of fire history, harvest history and stand age structures quantified the historical fire regime and identified the drivers of high stand densities in Chapter 2. Results revealed the dominance of an Indigenous influenced, high-frequency, lower-severity surface fire regime that burned individual sites every 11.6 years on average. Whereas low- and moderate-severity surface fires were common, high-severity crown fires were rare, having occurred only twice out of 623 fires spanning an 800-year period. This fire regime contributed to the persistence of large, fire-tolerant trees in canopies for hundreds of years, with moderate-severity surface fires driving understory death and renewal within stands. Moderate-severity fires initiated 49 of 51 documented cohorts and initiated all recent subcanopy cohorts.

Following initiation of recent cohorts, climate, harvesting, fires, and fire exclusion interacted to (i) remove biological legacies that were critical components of fire-resistant forest structures, (ii) promote higher intensity surface fires than would have occurred otherwise, (iii) promote higher numbers of regenerating trees in recent cohorts than would have occurred otherwise, (iv) remove fires that acted as negative, stabilizing feedbacks to tree regeneration, and (v) facilitate the persistence of dense subcanopy cohorts through time. Fire exclusion has affected all stands, with fires being absent for an average of 96 years, and as many as 140 years. As a result, all contemporary stands are outside the HRV of the historical fire regime. The

historical high-frequency, lower-severity fire regime and widespread occurrence of long-lived, highly scarred trees, including a ponderosa pine with 52 fire scars, are testament to Indigenous influences on the historical fire regime. Consequently, the prevention of Indigenous fire stewardship likely outweighs suppression of lightning-ignited fires in altering the fire regime.

In Chapter 3, I reconstructed a range of baseline metrics for historical stand configurations. These metrics were used to derive the HRV of contemporary dense, dry forests, which enabled quantification of contemporary dry forest degradation. Results revealed stands that were once low density and open canopied (range 76-354 trees ha⁻¹), dominated by large, fire-tolerant trees; stand basal area was dominated by shade-intolerant but fire-tolerant ponderosa pine and western larch (59%). Historical selective harvesting before 1951 reduced stand densities and stand basal area. The targeted removal of most large trees, and nearly all shade-intolerant species, had direct and immediate effects on stand structure and composition. Consequently, harvesting outweighed fire exclusion in shaping the structure and composition of contemporary stands. However, fire exclusion outweighed harvesting in driving stand development and landscape-scale densification by removing fires that historically maintained the metastability of low density stands.

The interactive effects of historical selective harvesting, post-harvest fires and fire-exclusion led to the generation of dense stands of small trees throughout the study area, and shifted compositions in favor of shade-tolerant Douglas-fir. Contemporary stands now average 2,730 live trees ha⁻¹, with shade-tolerant Douglas-fir dominating stand density and basal area. Moreover, western larch regeneration is absent, and ponderosa pine regeneration is negligible. Directional changes in contemporary stands over historical configurations align with other retrospective studies from the United States. However, the unregulated harvesting prior to 1951

resulted in greater relative changes in tree density, the dominance of small trees, and stand basal area occupied by shade-intolerant trees than has been previously reported. Overstory trees with small diameters (DBH < 7.5 cm but height > 1.3 m) now occupy up to 61% of live-tree stand basal area, highlighting a need to include small-diameter trees in stand structure assessments. None of the contemporary dense stands are within the HRV; two stands have shifted to an alternate state, and 18 stands are in transition. Consequently, all contemporary dense stands reflect degraded components of the dry forest matrix. The findings from Chapters 2 and 3 are synthesized visually in **Figure 5.1**.

Focusing on reconstructions of basal area increment in Chapter 4, I showed how past management practices, including selective harvest, fire suppression, and the prevention of Indigenous fire stewardship, have generated dense, unproductive stands throughout southeastern BC's dry forests. Trees in these stands are stressed: growth rates have declined, missing rings have increased, and many trees are dying. Canopy-dominant trees are more stressed than trees in the co-dominant and intermediate height classes, most likely caused by inverse asymmetric competition for soil moisture. Among species, western larch was most stressed, while Douglas-fir was least stressed owing to differences in life history attributes. Mortality of suppressed trees since the 1980s has eased competition, allowing Douglas-fir and ponderosa pine canopy-dominant trees to recover to above-average growth rates. However, western larch remains highly stressed. In these stagnant stands, thinning treatments to remove subcanopy trees are essential to alleviate competition and enhance the resilience of residual co-dominant and canopy dominant trees. Stands containing western larch should be prioritized to ensure its long-term persistence in the study area.

5.3 Implications for dry forest management and restoration

The trajectory of contemporary dense dry forests can only be realigned toward a path of resilience by proactive management through ecosystem restoration (Hessburg *et al.* 2015, Stephens *et al.* 2021, Hagsmann *et al.* 2021, Hessburg *et al.* 2021, Prichard *et al.* 2021). Restoration treatments that implement both heavy thinning and prescribed fire will enhance resilience under a lower-severity fire regime (Hessburg *et al.* 2019, Hagsmann *et al.* 2021, Prichard *et al.* 2021). The reconstructions of the historical fire regime (Chapter 2) and historical stand structure and composition (Chapter 3), and the species-specific thresholds of stress (Chapter 4) identified in this dissertation provide strong baselines for ecosystem restoration to enhance the resilience of contemporary dense, dry mixed-conifer forests in British Columbia.

Restoration of the historical fire regime must consider Indigenous fire stewardship. Since all stands have transitioned outside the HRV of the historical fire regime (Chapter 2), humans must create a new regime through prescribed fire to enhance dry forest resilience. Current classifications of dry forests in British Columbia recognize a historical, lower-severity surface fire regime (i.e., NDT4: Ecosystems with frequent stand-maintaining events, 4-50-year mean fire return intervals; BC Ministry of Forests 1995). However, the upper end of fire return intervals under this outdated classification overlaps with those defined for mixed-severity fire regimes in contemporary classifications (i.e., mixed-severity fire return intervals of 25-50 years; Marcoux *et al.* 2013, Hessburg *et al.* 2019). Moreover, an increasing number of fire regime reconstructions are identifying substantial human influences in areas previously inhabited or heavily utilized by Indigenous people (Barrett and Arno 1982, Lewis and Ferguson 1988, DeWilde and Chapin III 2007, Swetnam *et al.* 2016, Whitehair *et al.* 2018, Lake and Christianson 2019, Roos *et al.* 2021). Given the widespread inhabitation and utilization of dry forests by Indigenous people in

BC, their influences on historical fire regimes cannot be discounted. To reinstitute a new fire regime, prescribed fire programs must move beyond spring only fires at a fixed interval, and consider the seasonality and range of frequencies of historical fire regimes. Most importantly, prescribed fire programs must engage directly with Indigenous knowledge holders to understand WHY fires were set, as the reason for burning determined the seasonality, frequency, severity, size, and location of historical fires (Bonnicksen *et al.* 1999, Lake 2007, Prichard *et al.* 2021). Indigenous communities and land managers have a common interest in maintaining ecosystem resilience to climate change (Wong *et al.* 2020). By applying outcomes of natural science research derived from, and manipulating ecosystems within, traditional territories of Indigenous people, practitioners of ecosystem restoration have a social responsibility to engage Indigenous communities (Wong *et al.* 2020). Land managers must learn from Indigenous knowledge, collaborate with Indigenous people, and share the new knowledge generated through these collaborations to ensure the long-term success of restoration programs.

Restoration of historical stand structure and composition should retain biological legacies and components of contemporary stands that are within the HRV. Stand development in contemporary stands has slowed, and persistent subcanopy trees are outcompeting canopy-dominant trees for limited soil moisture. Stands with $\geq 28\%$ of stand basal area occupied by suppressed trees should be prioritized for restoration. Thinning from below, or low thinning, is required to remove sufficient sub-dominant trees to alleviate stress in canopy-dominant trees (Kerhoulas *et al.* 2013b, Sohn *et al.* 2016). Treatments should remove all trees in the suppressed height class, which are most abundant and stressed and drive stress among canopy-dominant trees. Co-dominant and intermediate trees are the least stressed and most vigorous, and therefore the most likely to exhibit growth releases following thinning (Oliver and Larson 1996).

Retaining larger co-dominant over smaller intermediate trees will likely yield greater productivity and enhance stand resilience to future fires (Agee and Skinner 2005). Canopy-dominant trees are important biological legacies and essential components of fire-resistant stand structures; all canopy-dominant trees should be retained. For stands that are transitioning out of the HRV of historical stand structure and composition, restoration treatments can build on the components of contemporary stands that are within the HRV to enhance stand resilience to fire and other disturbances. For example, ponderosa pine density and basal area in mixed-species (western larch-ponderosa pine-Douglas-fir) stands appear to have recovered or remained intact in most contemporary stands. Restoration treatments can retain these trees, but alter other stand components to align them with the HRV. The growth and vigor of retained trees should be monitored to assess effectiveness of thinning treatments and to adapt and optimize future treatments.

Although all stands will benefit from treatment, those including western larch should be prioritized to counter the severe decline of this species in the study area. Western larch canopy trees exhibited the highest levels of stress (Chapter 4), while regeneration was absent (Chapter 3). Moreover, episodes of missing rings and mortality will increase as climate change yields increasingly severe heat and drought events. Recently established protocols for promoting western larch adaptation to climate change include thinning as a primary tool (Crotteau *et al.* 2019). Based on my reconstructions, I recommend that all stands with ASDI >600 be thinned, and the relative basal area of suppressed trees reduced to <9%, if not eliminated. Monitoring will be essential, as western larch does not always respond to thinning (Schaedel *et al.* 2017). To ensure western larch persists into the future, additional efforts must focus on creating opportunities for new trees to establish.

5.4 Directions for future research

Below-ground dynamics are driving drought stress in canopy-dominant trees, and should be investigated further. Differences in the traits and adaptations of each species influence their ability to survive in dense stands (Chapter 4). Below-ground dynamics, particularly rooting depth, root grafting, hydraulic redistribution, and relationships with mycorrhizal networks are known to influence access to water.

While the relationships of tree size and rooting depth are well documented, and root grafting is well known and was commonly observed among Douglas-fir trees in stands, the influences of hydraulic redistribution and mycorrhizal networks in promoting access to water and driving stress were inferred from the literature. Future research should aim to understand the capacity for small subcanopy trees to benefit from the hydraulic redistribution of large canopy trees in dry forests. Specific efforts should be made to identify thresholds in the densities or BA of surrounding small trees at which hydraulic redistribution begins to stress large canopy trees.

Mycorrhizal networks are increasingly recognized as critical components of belowground functioning that connect distant trees. An abundance of research has shown that large trees can facilitate the growth of smaller trees by sharing resources with them through mycorrhizal networks (Simard *et al.* 1997, Beiler *et al.* 2009, Teste *et al.* 2009, Song *et al.* 2015, Simard 2017). However, it is unknown if this facilitative strategy can negatively impact large donor trees when there are many surrounding small trees that are benefiting. Future research on mycorrhizal networks should investigate if there is a limitation or threshold to this facilitative strategy, whereby large donor trees can become stressed by the demands of many smaller trees. Identifying thresholds in the capacity of large, canopy trees to support many small subcanopy trees through hydraulic redistribution and mycorrhizal networks will help identify stands that

require ecosystem restoration, and provide stand structure and composition targets for thinning treatments.

Rapidly changing climate will necessitate long-term monitoring, re-evaluation of restoration goals based on historical reference conditions, and adaptive management. Historical reconstructions in dry forests consistently document conditions with fewer trees, more open forest structures, a greater dominance of fire-tolerant species, and a frequent surface fire regime. Underlying these reconstructions is an assumption that past conditions were the result of disturbance processes that maintained a state of low-density, open-canopied forests (Hessburg *et al.* 2019). While in this state, species- and community-level adaptations promote ecosystem-wide resilience by resisting disturbances and stressors (Safford *et al.* 2012, Falk *et al.* 2019, Hessburg *et al.* 2019). However, broad-scale, human-driven changes in landscape structure and organization have decreased this resilience (Stevens-Rumann *et al.* 2018, Hessburg *et al.* 2019). Moreover, climate envelopes in many ecosystems are changing rapidly, and future conditions may not support forests within the historical range of variability (Keane *et al.* 2009, Higgs *et al.* 2014). Consequently, more aggressive tactics may be needed to realign the trajectory of dry forests with anticipated changes in climate (Higgs *et al.* 2014, Hessburg *et al.* 2019, Hagmann *et al.* 2021, Hessburg *et al.* 2021). For example, areas expected to have increased drought stress may require a reduction in closed-canopy forest, and an expansion of woodland or grassland (Hessburg *et al.* 2019). For managers aiming for long-term forest conservation, targeting the lower range of historical variability can be an ideal starting point (Stephens *et al.* 2021). Rather than being termed “ecosystem restoration,” these pro-active efforts are termed “ecosystem realignment,” with an overall goal of creating certainty and predictability in the future of our forests.

5.5 Figures

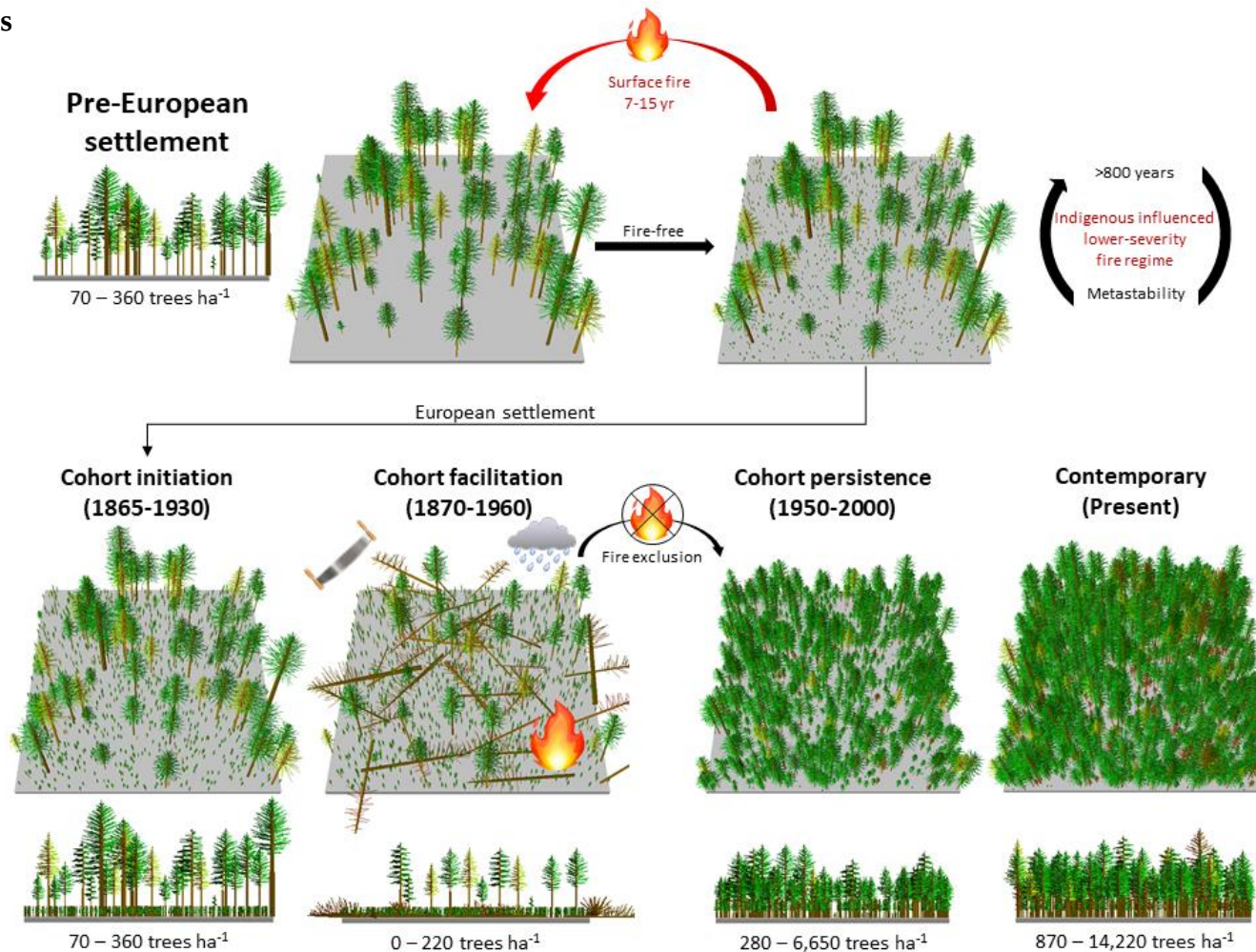


Figure 5.1 Visual synthesis of findings from Chapters 2 and 3.

The figure depicts historical stands under the influence of an Indigenous influenced, frequent, lower-severity surface fire regime, and how European settler practices of selective harvesting and fire exclusion shaped stand structure, composition, and stand development through time to promote dense stands throughout dry forests of southeastern British Columbia. Images were derived using the Stand Visualization System (v3.36, McGaughey 2004) through the R package *rSVS* (v.1.0.6, McCarter 2021).

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Appendices

Appendix A

Species-specific age to coring height regressions. A total of 78 whole-stem seedling and sapling samples were extracted from the most common tree species (i.e., Douglas-fir – PSME (n=35; height range 20-141cm), ponderosa pine – PIPO (n=28; height range 40-150 cm), western larch – LAOC (n=12; height range 57-150 cm) and lodgepole pine – PICO (n=18; height range 40-113 cm)). PSME were the oldest (12-70 yrs), PIPO and LAOC were intermediate in age (15-50 yrs and 20-36 yrs, respectively), and PICO were the youngest (2-22 yrs). Age-on-height regressions for all four species were significant ($p < 0.001$ for all species; all assumptions met). Regressions, model fit (r^2) and standard error of the estimates (SEE) for each species were as follows:

$$AGE_{PSME} = 0.358 * HEIGHT \ (r^2 = 0.90, \text{SEE} = 7.78)$$

$$AGE_{PIPO} = 0.268 * HEIGHT \ (r^2 = 0.93, \text{SEE} = 5.28)$$

$$AGE_{LAOC} = 0.188 * HEIGHT \ (r^2 = 0.93, \text{SEE} = 4.91)$$

$$AGE_{PICO} = 0.186 * HEIGHT \ (r^2 = 0.89, \text{SEE} = 2.81)$$

Appendix B

Estimated parameters and statistics associated with the linear regression model for historical tree establishment. Significance ($\alpha = 0.05$) was assessed using the SAS GLM Procedure (SAS Institute 2018).

Model: $\text{LN}(2012 - \text{Establishment Year}) = \text{DBH} * \beta_{\text{DBH}} + \beta_{\text{DBH Class}} + \beta_{\text{Species}} + \beta_{\text{Condition}}$

Average $R^2 = 0.74$

Plot	Model Fit			β_{DBH}	$\beta_{\text{DBH Class}}$				β_{Species}					$\beta_{\text{Condition}}$	
	n	P	R^2		D	M	P	S	Fd	Py	Lw	Pl	RMJ	L	D
PPX02	48	<0.0001	0.83	0.023	3.854	4.144	4.308	4.328	0	0.316	0	0	-0.491	0	0.327
PPX03	71	<0.0001	0.83	0.008	4.406	4.430	4.235	4.097	0	0.417	0	0	0	0	0.104
PPX04	53	<0.0001	0.47	0.015	4.639	4.452	4.637	4.785	0	0.072	0	0	0	0	-0.063
PPX07	90	<0.0001	0.64	0.011	4.676	4.501	4.574	4.618	0	0.157	0	0	0	0	0.017
PPX08	62	<0.0001	0.69	0.015	4.466	4.355	4.476	4.483	0	-0.013	0	0	0	0	0.027
PPX09	70	<0.0001	0.71	0.024	4.282	4.292	4.450	4.520	0	0.318	0	0	0	0	0.157
PPX10	54	<0.0001	0.90	0.016	4.435	4.197	4.094	4.178	0	-0.018	-0.143	0	0	0	-0.049
IDFX02	81	<0.0001	0.44	0.008	4.678	4.676	4.773	4.801	0	0.310	0.100	0	0	0	0.029
IDFX03	63	<0.0001	0.95	0.000	5.187	4.729	4.695	4.714	0	0.590	0	0	0	0	-0.008
IDFX04	52	<0.0001	0.81	0.046	2.681	3.365	3.622	3.862	0	0.080	0	0.499	0	0	0.126
IDFX05	59	<0.0001	0.69	0.024	4.047	4.071	4.305	4.387	0	0	0.080	0	0	0	-0.081
IDFX06	89	<0.0001	0.81	0.031	3.862	3.765	3.913	3.993	0	0	0.247	0	0	0	0.196
IDFX07	129	<0.0001	0.89	0.017	4.302	3.958	4.047	4.071	0	0.054	0.416	0	0	0	0.075
IDFX08	44	<0.0001	0.24	0.002	4.562	4.549	4.553	4.625	0	0	-0.025	0	0	0	-0.025
IDFX09	124	<0.0001	0.86	0.012	4.403	4.112	4.102	4.078	0	0.058	0.142	0.027	0	0	0.051
IDFX10	49	<0.0001	0.98	-0.005	5.904	4.004	4.078	4.121	0	0	0.358	0.262	0	0	-0.174
IDFX11	41	<0.0001	0.72	0.034	3.557	3.976	4.176	4.272	0	0.153	0	0	0	0	0.101
IDFX12	78	<0.0001	0.75	0.032	3.430	3.692	3.892	4.020	0	0.095	0.726	0	0	0	0.577
IDFX13	89	<0.0001	0.61	0.026	3.521	3.845	3.943	3.982	0	0	0.656	0	0	0	0.176
IDFX14	85	<0.0001	0.97	0.000	5.480	4.639	4.618	4.676	0	-0.398	0.133	0	0	0	-0.042

Appendix C

Estimated parameters and statistics associated with the linear regression model for historical tree age. Significance ($\alpha = 0.05$) was assessed using the SAS GLM Procedure (SAS Institute 2018).

$$\text{Model: LN(Age at bark)} = \text{DBH} * \beta_{\text{DBH}} + \beta_{\text{DBH Class}} + \beta_{\text{Species}} + \beta_{\text{Condition}}$$

Average $R^2 = 0.78$

Plot	Model Fit			β_{DBH}	$\beta_{\text{DBH Class}}$				β_{Species}					$\beta_{\text{Condition}}$	
	n	p	R^2		D	M	P	S	Fd	Py	Lw	Pl	RMJ	L	D
PPX02	48	<0.0001	0.82	0.023	3.854	4.144	4.313	4.316	0	0.313	0	0	-0.483	0	0.158
PPX03	71	<0.0001	0.82	0.008	4.402	4.427	4.222	4.050	0	0.432	0	0	0	0	-0.120
PPX04	53	<0.0001	0.59	0.015	4.641	4.452	4.638	4.783	0	0.072	0	0	0	0	-0.340
PPX07	90	<0.0001	0.68	0.011	4.644	4.490	4.578	4.575	0	0.163	0	0	0	0	-0.172
PPX08	62	<0.0001	0.72	0.015	4.472	4.359	4.473	4.488	0	-0.016	0	0	0	0	-0.155
PPX09	70	<0.0001	0.70	0.024	4.267	4.289	4.447	4.511	0	0.327	0	0	0	0	-0.050
PPX10	54	<0.0001	0.90	0.016	4.445	4.212	4.096	4.173	0	-0.025	-0.155	0	0	0	-0.289
IDFX02	81	<0.0001	0.54	0.009	4.656	4.665	4.767	4.798	0	0.311	0.101	0	0	0	-0.209
IDFX03	63	<0.0001	0.94	0.004	5.086	4.681	4.667	4.684	0	0.593	0	0	0	0	-0.214
IDFX04	52	<0.0001	0.81	0.046	2.669	3.353	3.624	3.862	0	0.080	0	0.508	0	0	0.075
IDFX05	59	<0.0001	0.77	0.024	4.049	4.067	4.320	4.282	0	0	0.119	0	0	0	-0.257
IDFX06	89	<0.0001	0.78	0.033	3.826	3.747	3.894	3.916	0	0	0.226	0	0	0	0.038
IDFX07	129	<0.0001	0.89	0.017	4.277	3.946	4.047	4.023	0	0.049	0.442	0	0	0	-0.137
IDFX08	44	<0.0001	0.70	0.003	4.499	4.560	4.563	4.305	0	0	-0.128	0	0	0	-0.157
IDFX09	124	<0.0001	0.87	0.012	4.400	4.113	4.118	4.060	0	-0.022	0.144	0.024	0	0	-0.169
IDFX10	49	<0.0001	0.98	-0.004	5.888	3.998	4.073	4.119	0	0	0.359	0.264	0	0	-0.382
IDFX11	41	<0.0001	0.73	0.038	3.385	3.915	4.137	4.238	0	0.140	0	0	0	0	-0.074
IDFX12	78	<0.0001	0.75	0.032	3.430	3.692	3.892	4.020	0	0.095	0.726	0	0	0	0.508
IDFX13	89	<0.0001	0.66	0.028	3.469	3.824	3.950	3.935	0	0	0.659	0	0	0	-0.049
IDFX14	85	<0.0001	0.97	0.001	5.438	4.633	4.612	4.645	0	-0.400	0.146	0	0	0	-0.194

Appendix D

Estimated parameters and statistics associated with the linear regression model to estimate Period

1 DBH in unsampled trees. Only plots containing live trees in reference years were analyzed.

Significance ($\alpha = 0.05$) was assessed using the SAS GLM Procedure (SAS Institute 2018).

Model: $DBH_{\text{Period 1}} = DBH * \beta_{DBH} + Age * \beta_{Age} + \beta_{\text{Species}} + \beta_{\text{Condition}}$

Average $R^2 = 0.79$

Plot	Model Fit			β_{DBH}	β_{Age}	β_{Species}					$\beta_{\text{Condition}}$	
	n	P	R^2			Fd	Py	Lw	Pl	RMJ	L	D
PPX02	11	<0.0001	0.91	0.498	0.075	-7.148	-7.495	0	0	0	*	*
PPX07	24	<0.0001	0.76	0.366	0.062	-10.781	-5.807	0	0	0	0	0.428
PPX10	24	<0.0001	0.38	0.285	0.114	-14.311	-20.004	-18.055	0	0	0	0
IDFX02	18	<0.0001	0.74	0.520	0.069	-14.241	-16.765	-15.662	0	0	0	0
IDFX03	10	<0.0001	0.85	0.524	0.040	-0.525	-3.069	0	0	0	0	4.117
IDFX04	9	<0.0001	0.88	0.407	-0.038	13.879	12.056	0	0	0	0	0
IDFX09	33	<0.0001	0.79	0.815	-0.007	-11.223	-3.921	-4.615	0	0	0	0
IDFX10	19	<0.0001	0.81	0.644	0.063	-14.922	0	-19.938	0	0	0	0
IDFX11	10	<0.0001	0.98	0.115	0.084	-5.182	-5.495	0	0	0	0	16.455
IDFX12	12	<0.0001	0.78	0.733	0.140	-35.894	-48.698	-37.972	0	0	0	8.103
IDFX14	25	<0.0001	0.82	0.698	0.126	-31.461	-44.760	-34.550	0	0	0	0

* The variable “Condition” was dropped from the PPX02 model because no dead ponderosa pine individuals were alive in the Period 1 reference year.

Appendix E

Estimated parameters and statistics associated with the linear regression model to estimate Period 2 DBH in unsampled trees. Only plots containing live trees in reference years were analyzed.

Significance ($\alpha = 0.05$) was assessed using the SAS GLM Procedure (SAS Institute 2018).

Model: $DBH_{\text{Period 2}} = DBH * \beta_{DBH} + Age * \beta_{Age} + \beta_{\text{Species}} + \beta_{\text{Condition}}$

Average $R^2 = 0.97$

Plot	Model Fit			β_{DBH}	β_{Age}	β_{Species}					$\beta_{\text{Condition}}$	
	n	P	R^2			Fd	Py	Lw	Pl	RMJ	L	D
PPX02	42	<0.0001	0.93	0.690	0.055	-6.852	-4.874	0	0	0	0	1.444
PPX07	83	<0.0001	0.96	0.662	0.067	-9.451	-10.120	0	0	0	0	2.951
PPX10	35	<0.0001	0.99	0.751	0.056	-5.869	-6.282	-6.433	0	0	0	2.890
IDFX02	81	<0.0001	0.95	0.684	0.048	-6.383	-8.844	-4.782	0	0	0	2.150
IDFX04	31	<0.0001	0.98	0.802	0.037	-8.380	-6.416	0	0	0	0	2.990
IDFX06	30	<0.0001	0.95	0.961	-0.009	-4.978	0	-1.492	0	0	0	1.775
IDFX11	16	<0.0001	0.99	0.606	0.062	-7.502	-12.645	0	0	0	0	5.032
IDFX14	85	<0.0001	0.99	0.716	0.057	-6.557	-11.330	-8.076	0	0	0	2.220

Appendix F

The percentage of density and basal area occupied by different species in Period 1, Period 2, and Contemporary stand reconstructions.

Species include ponderosa pine (PIPO), western larch (LAOC), and Douglas-fir (PSME). “Other” species includes lodgepole pine and Rocky Mountain juniper.

Plot	Period 1									Period 2									Contemporary							
	Year	Density (%)				BA (%)				Year	Density (%)				BA (%)				Density (%)				BA (%)			
		PSME	PIPO	LAOC	Other	PSME	PIPO	LAOC	Other		PSME	PIPO	LAOC	Other	PSME	PIPO	LAOC	Other	PSME	PIPO	LAOC	Other	PSME	PIPO	LAOC	Other
PPX02	1917	65.1	34.9	0.0	0.0	15.4	84.6	0.0	0.0	1959	82.4	17.6	0.0	0.0	73.1	26.9	0.0	0.0	61.6	18.4	0.0	20.0	80.7	17.5	0.0	1.8
PPX03	1922	3.9	96.1	0.0	0.0	10.6	89.4	0.0	0.0	-	-	-	-	-	-	-	-	-	49.3	50.7	0.0	0.0	75.2	24.8	0.0	0.0
PPX04	1912	87.9	12.1	0.0	0.0	60.3	39.7	0.0	0.0	1962	99.8	0.2	0.0	0.0	98.3	1.7	0.0	0.0	99.7	0.3	0.0	0.0	98.3	1.7	0.0	0.0
PPX07	1907	46.9	53.1	0.0	0.0	36.1	63.9	0.0	0.0	1955	77.0	23.0	0.0	0.0	50.4	49.6	0.0	0.0	77.8	22.2	0.0	0.0	61.6	38.4	0.0	0.0
PPX08	1912	84.0	16.0	0.0	0.0	58.3	41.7	0.0	0.0	1969	69.9	30.1	0.0	0.0	34.2	65.8	0.0	0.0	66.8	33.2	0.0	0.0	37.8	62.2	0.0	0.0
PPX09	1915	18.6	81.4	0.0	0.0	31.4	68.6	0.0	0.0	1966	89.7	10.3	0.0	0.0	83.3	16.7	0.0	0.0	90.3	9.7	0.0	0.0	89.2	10.8	0.0	0.0
PPX10	1917	55.6	11.9	32.5	0.0	22.6	30.2	47.1	0.0	1980	51.9	18.4	29.8	0.0	58.8	23.5	17.7	0.0	74.6	14.8	10.6	0.0	54.3	26.0	19.7	0.0
IDFX02	1909	49.4	34.0	15.7	0.0	34.9	2.2	62.6	0.0	1953	98.1	1.8	0.1	0.0	92.4	6.7	1.0	0.0	97.8	2.1	0.1	0.0	92.7	6.6	0.7	0.0
IDFX03	1922	14.7	85.3	0.0	0.0	14.5	85.5	0.0	0.0	-	-	-	-	-	-	-	-	-	100.0	0.0	0.0	0.0	99.6	0.4	0.0	0.0
IDFX04	1917	55.2	8.5	36.4	0.0	32.7	7.4	59.9	0.0	1978	13.2	86.8	0.0	0.0	27.4	72.6	0.0	0.0	54.3	44.0	0.0	1.7	31.4	66.7	0.0	2.0
IDFX05	1907	83.4	0.0	16.6	0.0	84.9	0.0	14.6	0.0	-	-	-	-	-	-	-	-	-	85.2	0.0	14.8	0.0	77.5	0.0	22.5	0.0
IDFX06	-	-	-	-	-	-	-	-	-	1964	16.7	0.0	83.3	0.0	40.8	0.0	54.6	0.0	95.4	0.0	4.6	0.0	90.0	0.0	10.0	0.0
IDFX07	1937	34.2	5.4	60.3	0.0	29.1	4.2	66.7	0.0	-	-	-	-	-	-	-	-	-	97.3	0.8	1.9	0.0	87.8	7.6	4.6	0.0
IDFX08	1914	58.0	0.0	42.0	0.0	63.8	0.0	36.2	0.0	-	-	-	-	-	-	-	-	-	64.6	0.0	35.4	0.0	70.0	0.0	30.0	0.0
IDFX09	1942	58.2	0.7	41.2	0.0	48.1	1.1	50.9	0.0	-	-	-	-	-	-	-	-	-	93.4	0.7	4.6	1.3	82.1	1.9	13.9	2.0
IDFX10	1949	42.7	0.0	57.3	0.0	24.1	0.0	75.9	0.0	-	-	-	-	-	-	-	-	-	34.4	0.0	63.2	2.4	38.6	0.0	60.1	1.2
IDFX11	1919	58.0	33.3	8.6	0.0	39.8	36.2	24.1	0.0	1959	94.3	5.7	0.0	0.0	73.2	26.8	0.0	0.0	98.9	1.1	0.0	0.0	89.3	10.7	0.0	0.0
IDFX12	1919	54.3	7.6	38.1	0.0	61.8	16.7	21.6	0.0	-	-	-	-	-	-	-	-	-	93.5	2.6	3.9	0.0	76.7	9.5	13.8	0.0
IDFX13	1922	46.9	0.0	53.1	0.0	50.1	0.0	49.9	0.0	-	-	-	-	-	-	-	-	-	94.8	0.0	5.2	0.0	88.9	0.0	11.1	0.0
IDFX14	1919	61.4	3.9	34.6	0.0	29.5	9.5	60.9	0.0	1977	90.1	0.0	9.9	0.0	85.2	0.5	14.0	0.3	90.1	0.1	9.8	0.1	87.7	0.7	11.4	0.2

Appendix G

Reconstructed, pre-harvest plot-level density of ponderosa pine trees in 5 cm DBH classes used for baseline and HRV reconstructions.

Plot	Zone	DBH Class (cm)																									
		5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130
PPX02	PP	0	2	0	7	4	3	1	0	5	2	2	2	2	2	0	0	0	0	0	2	4	0	0	0	0	0
PPX03	PP	0	0	0	27	28	2	0	2	4	0	2	4	2	0	2	0	0	0	0	0	0	0	0	0	0	0
PPX04	PP	0	2	0	2	0	0	2	0	0	0	4	2	0	2	2	0	2	4	4	0	4	0	0	0	0	0
PPX07	PP	0	38	19	20	26	0	2	6	4	0	6	4	2	10	6	2	0	0	2	0	2	0	0	0	0	0
PPX08	PP	2	1	1	2	2	1	4	4	2	14	4	2	2	0	0	0	0	0	2	0	0	0	0	0	0	0
PPX09	PP	13	0	0	2	11	17	14	28	26	14	14	2	2	2	2	0	0	0	2	0	0	0	0	0	0	0
PPX10	PP	0	1	5	8	5	0	1	0	0	2	0	0	2	4	10	2	2	0	0	0	0	0	0	0	0	0
IDFX02	IDF	38	39	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX03	IDF	0	0	0	3	12	34	24	40	20	20	6	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX04	IDF	0	0	0	0	4	3	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX05	IDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX06	IDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX07	IDF	0	0	0	0	1	6	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX08	IDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX09	IDF	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX10	IDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX11	IDF	0	1	3	0	0	25	1	2	2	4	8	4	0	2	2	0	0	0	0	0	0	0	0	0	0	0
IDFX12	IDF	0	0	0	1	2	1	0	0	2	2	0	0	0	0	0	2	0	2	0	0	0	2	0	0	0	0
IDFX13	IDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX14	IDF	0	0	1	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0

Appendix H

Reconstructed, pre-harvest plot-level density of western larch trees in 5 cm DBH classes used for baseline and HRV reconstructions.

Plot	Zone	DBH Class (cm)																									
		5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130
PPX02	PP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PPX03	PP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PPX04	PP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PPX07	PP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PPX08	PP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PPX09	PP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PPX10	PP	0	49	0	4	4	2	6	6	8	6	10	2	6	4	4	0	0	2	2	0	0	0	0	0	0	0
IDFX02	IDF	2	2	0	0	3	2	0	0	6	2	2	4	4	0	2	4	2	2	0	0	0	0	0	0	0	0
IDFX03	IDF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX04	IDF	0	0	0	8	6	0	18	4	8	2	2	4	4	0	2	0	2	0	0	0	0	0	0	0	0	0
IDFX05	IDF	1	0	0	6	2	4	0	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX06	IDF	30	124	0	4	6	20	25	8	7	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX07	IDF	1	0	0	6	17	21	30	14	6	6	4	2	2	0	0	0	0	0	2	0	0	0	0	0	0	0
IDFX08	IDF	0	0	0	4	4	6	14	6	10	10	4	2	2	0	0	0	2	2	2	0	0	0	0	0	0	0
IDFX09	IDF	0	0	1	6	4	5	17	13	10	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX10	IDF	0	0	0	0	2	1	8	11	12	12	12	8	12	2	0	0	2	0	0	0	0	0	0	0	0	0
IDFX11	IDF	0	0	0	0	0	0	0	2	0	2	0	2	0	4	2	0	0	0	2	0	0	0	0	0	0	0
IDFX12	IDF	0	0	29	15	0	2	1	2	4	8	4	2	2	0	0	2	0	0	0	0	0	0	0	0	0	0
IDFX13	IDF	0	0	0	25	0	2	0	4	0	6	8	14	4	2	0	0	2	0	2	0	0	0	0	0	0	0
IDFX14	IDF	0	0	1	0	2	8	1	6	0	4	6	2	4	4	2	0	2	2	0	0	0	0	0	0	0	0

Appendix I

Reconstructed, pre-harvest plot-level density of Douglas-fir trees in 5 cm DBH classes used for baseline and HRV reconstructions.

Plot	Zone	DBH Class (cm)																									
		5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130
PPX02	PP	0	6	36	20	3	1	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PPX03	PP	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
PPX04	PP	11	28	82	28	2	3	8	8	6	4	4	8	12	2	6	4	0	0	0	0	0	0	2	0	0	0
PPX07	PP	19	17	56	8	3	2	1	4	2	6	2	2	0	4	0	0	4	0	0	2	0	0	0	0	0	0
PPX08	PP	53	40	76	14	3	1	2	4	8	8	2	4	0	6	2	2	0	0	0	0	0	0	0	0	0	2
PPX09	PP	1	0	1	2	0	0	0	0	4	2	2	8	4	6	4	0	0	0	0	0	0	0	0	0	0	0
PPX10	PP	0	31	117	0	29	0	4	6	2	2	0	2	2	0	0	0	2	0	0	0	0	0	0	0	0	0
IDFX02	IDF	73	1	10	5	4	2	1	6	2	2	4	0	4	0	0	0	0	2	0	0	0	0	0	0	0	0
IDFX03	IDF	0	0	0	0	3	7	8	0	4	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX04	IDF	0	22	22	2	7	20	10	0	4	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
IDFX05	IDF	0	11	6	3	5	7	14	22	16	18	4	14	6	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX06	IDF	0	0	3	1	7	14	4	6	0	2	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX07	IDF	8	5	4	2	10	12	7	4	0	2	4	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0
IDFX08	IDF	0	0	0	0	2	0	8	10	20	10	14	14	4	6	2	0	2	0	0	2	0	0	0	0	0	0
IDFX09	IDF	0	0	1	2	42	12	15	3	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IDFX10	IDF	0	0	0	0	25	25	2	0	0	3	4	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
IDFX11	IDF	8	32	13	1	1	1	0	0	27	2	3	2	0	2	0	0	0	0	0	0	2	0	0	0	0	0
IDFX12	IDF	0	0	2	0	16	9	7	7	22	8	4	14	2	2	0	4	2	0	0	0	2	0	0	0	0	0
IDFX13	IDF	0	0	0	0	1	5	1	10	10	8	10	8	2	0	4	2	0	0	0	0	0	0	0	0	0	0
IDFX14	IDF	1	0	0	14	29	18	10	2	1	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix J

Baseline and Contemporary metrics of stand density, BA, and QMD for HRV reconstructions.

The mean ($\pm$ SD) and ranges of values are provided for each metric. Species include ponderosa pine (PIPO), western larch (LAOC), and Douglas-fir (PSME).

Species Assemblage	Baseline			Contemporary		
	Density (ha^{-1})	BA (m^2ha^{-1})	QMD (cm)	Density (ha^{-1})	BA (m^2ha^{-1})	QMD (cm)
PIPO-PSME	193.7 (± 78.7)	19.7 (± 9)	35.7 (± 4.9)	3981.7 (± 4841.5)	29.4 (± 7.8)	13.1 (± 5)
	76-281.5	6.4-31	28.4-43.5	874-14219	18.5-40.7	5.8-19.4
LAOC-PSME	170.9 (± 56.3)	21.2 (± 6.9)	40.9 (± 10.4)	2041.7 (± 994.6)	32 (± 8.3)	15.1 (± 3.8)
	130-269.5	11.6-30.5	23.4-49	1004-3343	22.2-40.4	10.7-20
LAOC-PIPO-PSME	195 (± 71.6)	18.9 (± 6.8)	35.4 (± 5.3)	2063.8 (± 884)	30 (± 8.2)	13.9 (± 1.5)
	127-354	11.6-29.9	28.4-44.4	1163-3827	19-41.2	11.7-16.8

Appendix K

Baseline and Contemporary metrics of species density and BA for HRV reconstructions. The mean ($\pm$ SD) and ranges of values are provided for each metric. Species include ponderosa pine (PIPO), western larch (LAOC), and Douglas-fir (PSME).

Species Assemblage	Baseline						Contemporary					
	Density (ha^{-1})			BA (m^2ha^{-1})			Density (ha^{-1})			BA (m^2ha^{-1})		
	PSME	PIPO	LAOC	PSME	PIPO	LAOC	PSME	PIPO	LAOC	PSME	PIPO	LAOC
PIPO-PSME	101.5 ($\pm$ 91.6)	92.1 ($\pm$ 59.2)	-	7.4 ($\pm$ 6.3)	12.3 ($\pm$ 5.3)	-	3625.6 ($\pm$ 4968.9)	331.1 ($\pm$ 276.6)	-	22.1 ($\pm$ 7.8)	7.2 ($\pm$ 8.9)	-
	3-225	30-163	-	0.7-18.7	5.7-18.5	-	520-14216	3-662	-	14.9-37.4	0.2-25.3	-
LAOC-PSME	77.4 ($\pm$ 32.5)	-	93.7 ($\pm$ 76.2)	11.5 ($\pm$ 6.6)	-	9.6 ($\pm$ 5.1)	1536.2 ($\pm$ 1054.2)	-	493.9 ($\pm$ 609.9)	24.5 ($\pm$ 11.2)	-	7.5 ($\pm$ 4)
	45-126	-	25-224.5	4.7-19.5	-	2.8-16	649-3188.5	-	56-1561	8.6-35.1	-	3.8-13.3
LAOC-PIPO-PSME	103.4 ($\pm$ 40.9)	27.5 ($\pm$ 28.2)	64.2 ($\pm$ 34.8)	7.2 ($\pm$ 4.4)	3.1 ($\pm$ 3.5)	8.7 ($\pm$ 3.1)	1840.7 ($\pm$ 958.6)	144.7 ($\pm$ 233)	72.6 ($\pm$ 92.5)	23.4 ($\pm$ 10.5)	4.2 ($\pm$ 4.4)	2.3 ($\pm$ 2.3)
	63-197	1-80	14-115	4.6-17.7	0.1-9	4.8-14.1	800-3743	1-648	0-246	6-38.2	0.2-12.7	0-6.8

Appendix L

Harvest metrics of density and BA for HRV reconstructions. The mean ($\pm$ SD) and ranges of values are provided for each metric. Species include ponderosa pine (PIPO), western larch (LAOC), and Douglas-fir (PSME).

Species Assemblage		Harvested Structure (%)	
		Density (ha^{-1})	BA (ha^{-1})
PIPO-PSME	mean ($\pm$ SD)	73.5 ($\pm$ 27.9)	90.8 ($\pm$ 11.8)
	range	23.7-96	66.3-99
LAOC-PSME	mean ($\pm$ SD)	67.2 ($\pm$ 33.6)	85.9 ($\pm$ 17.7)
	range	18.6-100	58.9-100
LAOC-PIPO-PSME	mean ($\pm$ SD)	53.1 ($\pm$ 21.7)	82.2 ($\pm$ 13.4)
	range	24.7-92.1	57-94.8