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Ecological legacies of fire detected using plot-level measurements and LiDAR in an old growth coastal temperate rainforest

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ABSTRACT

Vegetation succession following fire disturbances has long been of interest in ecology, but the evolution of landscape pattern and structure following low-severity ground fires is poorly understood. In coastal temperate rainforest ecosystems historic fire disturbances are not well documented and time since the most recent fire is largely unknown. We sampled 6000 tree cores from 27 forest plots that burned 124 years ago and 11 plots with no recent history of fire (within the last 1000 years) to understand the legacies of fire on forest stand structure in a British Columbia high-latitude coastal temperate rainforest. We assessed the timing and spatial extent of historic fires with a 700 year fire history reconstruction built from fire scars, and applied light detection and ranging (LiDAR) to ground-truth plot-level measurements. We sampled an additional 32 plots with known fire histories to validate the ability of LiDAR to detect and characterize historic fire legacies. In total, we sampled 70 plots for stem density, stand structure, and stand composition. Trees in burned plots were significantly taller, and the mean stem density was less than half that of unburned plots despite 124 years since the most recent fire. LiDAR analyses had similar results and also showed that burned plots had lower canopy cover and greater canopy complexity. Field-based measurements are still required to resolve differences in community structure and composition in our temperate rainforest study area. However, LiDAR may be an important tool to bridge the spatial information offered by plot-level measurements to larger area characterizations in the future. Our comparative analyses provide an improved understanding of fire legacies and temperate rainforest structure, which increases our ability to detect fire disturbances in heterogeneous forests and is important for forest resource management and conservation.

1. Introduction

Ecological memory or the degree to which a landscape is shaped by its past patterns and processes is important to how ecosystems respond to disturbance and can be identified in the physical structure of vegetation, soil substrate, and resource availability (White and Pickett, 1985; Peterson, 2002; Johnstone et al., 2016). Fire can be both a natural and anthropogenic disturbance that is nearly ubiquitous in terrestrial ecosystems (Bowman et al., 2009; Whitlock et al., 2010). Fire affects successional vegetation patterns by opening canopies, consuming horizontal and vertical fuels, preparing seedbeds, and changing soil substrate and water hydrology (McKenzie and Kennedy, 2011; Bolton et al., 2015). Although the feedback between fire and landscape pattern is ecosystem specific (Bowman et al., 2011), recently burned forests often have characteristic patterns of spatial variability that can be detected with remote sensing techniques such as light detection and ranging (LiDAR; McKenzie and Kennedy, 2011). Nevertheless, we have little understanding of how these patterns change over larger spatial and longer temporal scales, specifically when fire disturbances are low-severity and much of the forest structure remains intact as standing live trees (Falkowski et al., 2010; Goetz et al., 2010; Krasnow et al., 2016). The rate of vegetation recovery and legacies of fire disturbance depends on several factors including time elapsed since the most recent fire event (TSF), and the fire frequency, fire severity, fire extent, and fire-sensitivity of vegetation (Foster et al., 1998; Johnstone et al., 2016; Stevens-Rumann and Morgan, 2016). Species life histories and local site factors such as topography also influence vegetation recovery (Foster et al., 1998; Bartels et al., 2016).

Ecologists are often challenged by the scale limitations of field assessments, which constrain their ability to compare plot-level

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measurements to landscape level processes (Swetnam et al., 2015). This is especially true in heterogeneous landscapes characterized by patch dynamics where plot-level measurements provide important inventories of historic disturbances and vegetation succession, but are limited in their spatial application (Foster et al., 1998). Fortunately, the capacity to locate and characterize historic fire disturbances is increasing with the widespread availability of remote sensing techniques such as LiDAR, which provide site-specific measurements and regional characterization of vegetation (Lim et al., 2003; White et al., 2016). LiDAR has the potential to greatly advance the spatial area of vegetation measured following disturbance, particularly canopy height metrics, and associated biomass (Houghton et al., 2009; Goetz et al., 2010; Bolton et al., 2015; Nijland et al., 2015). However, the potential of this technology to reconstruct historic fire disturbances remains largely untested, especially in complex and heterogeneous landscapes where natural variability in forest structure is high (Swetnam et al., 2011). This is especially true of high-latitude coastal temperate rainforests like those in British Columbia, Canada, where historic fire disturbances are not well documented (Daniels and Gray, 2006; Hoffman et al., 2016a, 2016b, 2017).

Analyses that assess a range of spatial scales from small patches to broader, landscape-level legacies are important when studying disturbances such as fire which are controlled by several processes operating at different scales (Falk et al., 2007). Quantifying relationships between fire history and forest structure across large forested areas may provide an improved understanding of both spatial and temporal variability in heterogeneous coastal temperate rainforests, which is important for ongoing forest resource management (Tepley et al., 2013). We use airborne LiDAR and plot-level measurements to assess differences in burned and unburned forests in a high-latitude temperate rainforest on the Central Coast of British Columbia. We ask the following questions: (1) What fire legacies are apparent in forest stand structure and composition after a 124 year post-fire period? (2) How does historic fire activity affect regeneration dynamics through changes to canopy structure and stand density? (3) Can LiDAR detect differences in forest stand structure that are apparent in plot-level measurements? We hypothesize that historically burned forests remain more open, have higher conifer diversity and contain lower-density stands with taller and wider trees.

2. Methods

2.1. Study area

The study area encompasses a 20 km^2 area located on Hecate and Calvert Islands (North 51° 39 Latitude, West 128° 04 Longitude) within the Hakai Lúxvbálís Conservancy on the Central Coast of British Columbia, Canada (Fig. 1). The coastal margin of British Columbia has many small islands characterized by exposed and rocky homogenous quartz diorite and granodiorite bedrock, subdued terrain, and elevations ranging from sea level to approximately 1000 m (Roddick, 1996). Cool temperatures (average annual ~ 7 °C, average summer ~ 12 °C) coupled with locally abundant (~4000 mm) and year-round rainfall distinguish this temperate climate region (Banner et al., 1993, 2005). The study area is located within the very wet hypermaritime subzone (CHWvh2) of the Coastal Western Hemlock biogeoclimatic classification (Meidinger and Pojar, 1991).

Excess soil water regulates this environment and subtle variations in slope or drainage result in significant differences in forest productivity (Banner et al., 2005). Although several vegetation types have been categorized in the study area (Thompson et al., 2016), four types dominate along a gradient of productivity and are defined by species and closely associated landforms (Banner et al., 1993, 2005). Productive (zonal) forests are found in nearshore and riparian areas with large-diameter western redcedar (*Thuja plicata* Donn ex D. Don.) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and lesser amounts of yellow-cedar (*Cupressus nootkatensis* [D.Don] Farjon and Harder), and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) (Meidinger and Pojar, 1991). Bog forests exhibit stunted growth forms and are located on hill slopes dominated by western redcedar, yellow-cedar, western hemlock, and shore pine (*Pinus contorta* var. *contorta* Douglas ex Louden) (Klinka et al., 1996). Bog woodlands are the most common vegetation type in the study area and are comprised of patchy mosaics of forested and unforested sites in subdued or rolling terrain (Thompson et al., 2016). These forests contain roughly equal densities of western redcedar, yellow-cedar, and shore pine with lesser amounts of mountain hemlock (*Tsuga mertensiana* [Bong.]) (Klinka et al., 1996). Blanket bogs are nutrient-poor, sparsely forested wetland areas that contain small amounts of shore pine and yellow-cedar (Banner et al., 1993).

Compared to most of British Columbia, the Central Coast has experienced very small fluctuations in sea levels (± 2 m) during the Holocene (Shugar et al., 2014). This allowed First Nations to continuously inhabit the region for > 13,000 years until European contact in the late 18th and 19th centuries, which decreased First Nations activities in their traditional territories (McLaren et al., 2014, 2015). Lightning-ignited fires are rare and First Nations likely played an important role in igniting fires and controlling the spatial and temporal aspects of fire activity (Hoffman et al., 2016a, 2016b). Ongoing research suggests that fire in the study area may have been intentionally used as a tool for resource management (Trant et al., 2016; Hoffman et al., 2017), but little specific ethnographic information is available regarding how First Nations used fire to control vegetation succession (Turner, 1999, 2014). Historic fire events were composed of low- and mixed-severity ground fires that did not result in significant stand mortality (Hoffman et al., 2017). Although more than a century has passed since the most recent fire event, the ecological legacies of historic fire activity, such as fire-scarred trees and even-aged cohorts remain visible in the study area today. Colonists never settled the region and there is no history of industrial logging or mining (McLaren et al., 2015).

2.2. Ecological field sampling

Terrestrial ecosystem maps and satellite imagery taken in 2012 were used to select the locations of 70 plots (11.28 m radius [0.04-ha]) with a stratified random sampling design representing the range of elevations, aspects, slopes, and four dominant vegetation types on Hecate and Calvert Islands (Fig. 1). Twenty-seven plots were sampled within a low- and mixed-severity 287-ha fire on Hecate Island that most recently burned in 1893 (Fig. 1, hereafter 'burned' plots). Forest structure in burned plots was previously reconstructed with a network of 45 living fire-scarred trees (containing 99 fire scars) and 4000 tree cores (Hoffman et al., 2016b, 2017). Burned plots experienced repeated low- and mixed-severity fires of varying sizes (0.01–287-ha) from the first detected fire in 1376 until the last detected fire in 1893 (Hoffman et al., 2016b). The 1893 fire affected all 27 burned plots and these plots experienced an average of five fire events between 1376 and 1893 (Appendix A: Table 1). The 27 burned plots were compared to 11 plots that were selected and sampled with the same methods, but contained no fire scars and had no aboveground evidence of fire activity (hereafter 'unburned' plots) on Hecate and Calvert Islands (Fig. 1). Field surveys and the collection and crossdating of an additional 2000 tree cores from the unburned plots confirmed the absence of fire scars and post-fire cohorts. This information together with previous radiocarbon dating of charcoal from historic fires deposited in soils confirmed that the 11 unburned plots had not experienced fire activity for at least 1000 years (Hoffman et al., 2016a). This design allowed for comparison of plots with similar forest stand structure, vegetation, and topographical position but with differing fire histories. Time and financial constraints limited the ability to perform a balanced sampling design.

In all plots, two 5 mm increment cores were sampled from the bases (~15 cm height) of all trees > 7.5 cm diameter at breast height (dbh).

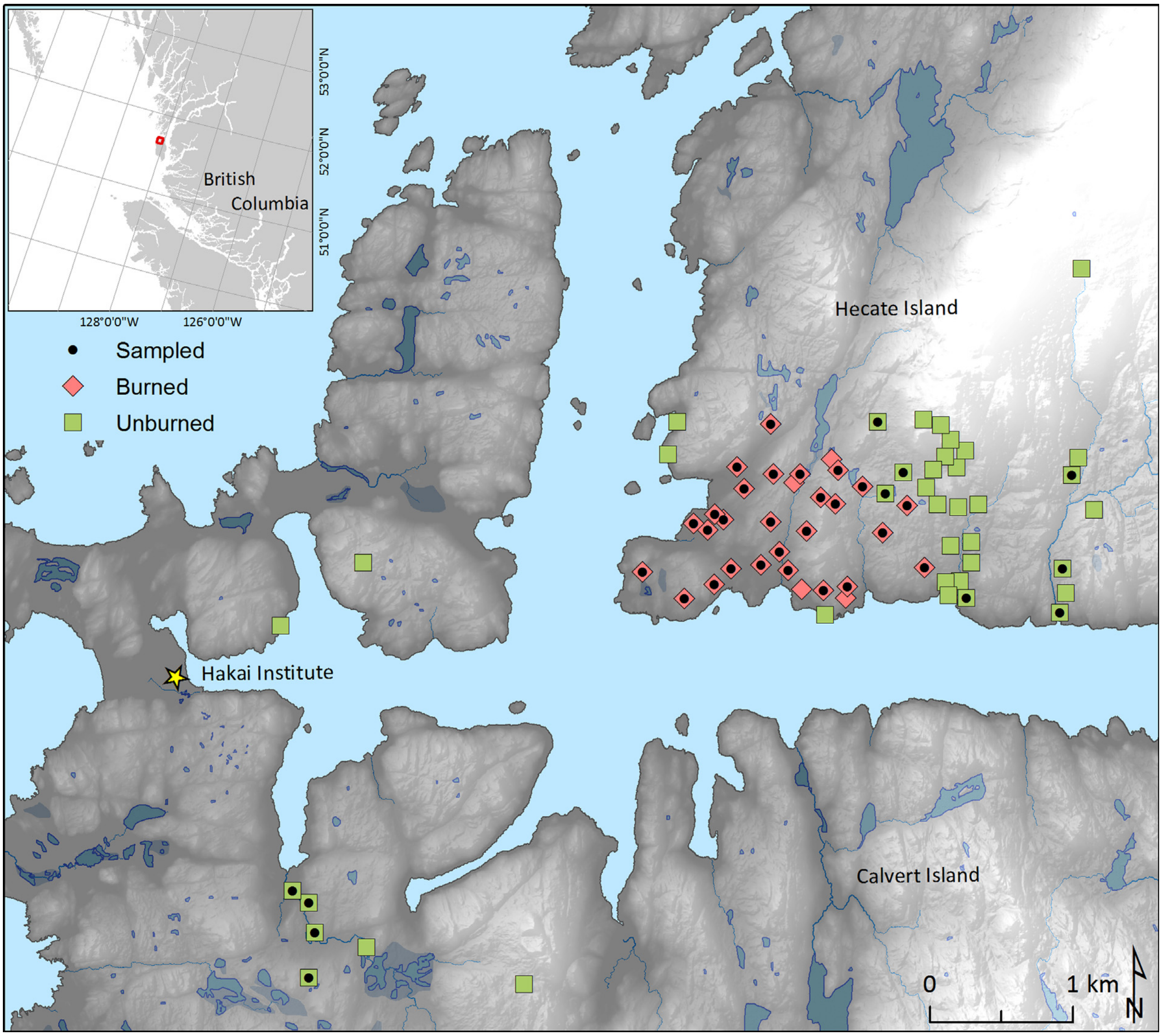

Fig. 1. The study area encompasses a 20 km^2 area located on Hecate and Calvert Islands (North 51° 39, West 128° 04). Burned plots (red diamond symbol) on Hecate Island are within a low- and mixed-severity 287-hectare fire dated with fire-scarred trees to 1893. Sampled burned plots (27) contain a black circle within the red diamond symbol. Unburned vegetation plots (green square) are located on Hecate and Calvert islands and have no evidence of aboveground fire activity (within the last 1000 years). Sampled unburned plots (11) contain a black circle within the green square symbol. Seventy plots were randomly selected, ground-truthed for fire evidence, and included in the LiDAR analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The dbh of all trees was measured at 1.3 m from the tree base and the height and species were also recorded. To assess differences in forest regeneration in plots, all saplings (< 7.5 cm dbh, > 15 cm height) and seedlings (< 15 cm height) were characterized (by species, height, and dbh), counted and then destructively sampled in five, 3 m^2 subplots. A diagram of how subplots were sampled is detailed in Appendix A: Fig. A1.

In the laboratory, fire scars, tree cores, and sapling discs were processed using standard dendrochronological techniques (Stokes and Smiley, 1968). Samples were measured and counted using a Velmex® sliding stage micrometer (precision 0.001 mm) and then statistically verified using the computer program COFECHA (Grissino-Mayer, 2001). For cores that did not reach pith, we used Duncan's (1989) method to calculate the distance to the chronological centre of each tree. The exact year of fire events was determined by crossdating fire scar wedges and tree rings from post-fire cohorts (Johnson and Gutsell, 1994). For age structure analyses, we binned trees together by decade to reduce uncertainty in time to reach coring height (Tepley and Veblen, 2015). We calculated the density of all seedlings, saplings, and trees in four dbh classes in every plot and all plots were assessed with airborne laser scanning.

2.3. LiDAR sampling

In addition to the 27 burned and 11 unburned plots, we randomly selected 32 plots (11.28 m radius [0.04-ha]) that were stratified within the four vegetation types and assessed with LiDAR (Fig. 1). The 32 additional plots were ground-truthed to confirm the presence or absence of fire, but no plot-level measurements of forest stand structure were sampled. Of the 32 additional plots assessed, four plots contained historically burned forests and 27 plots had no aboveground evidence of fire (Fig. 1). In total, 70 plots were utilized to characterize historic fire disturbances.

2.4. LiDAR data

Discrete return airborne scanning LiDAR was acquired across Hecate and Calvert Islands in August 2012 by Terra Remote Sensing Inc. (Sidney, BC, Canada). LiDAR was collected from 1150 m AGL at 100 kHz with a maximum scan angle of 26°. The resulting point data

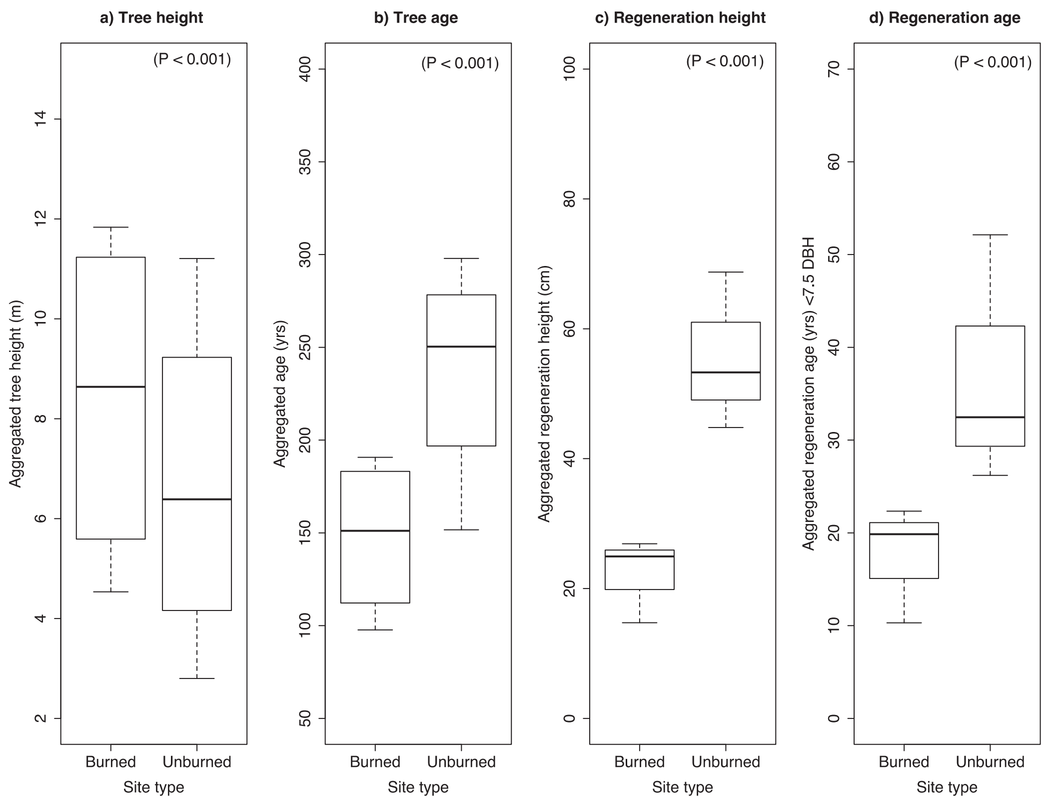

Fig. 2. The results of the two factor model nested analysis of variance (ANOVA) with unequal sample sizes. Box and whisker plots describe differences in (a) mature tree height in metres, (b) tree age in years, (c) regenerative tree height in metres and (d) regenerative tree age in years between burned and unburned forest plots aggregated across four vegetation types (zonal forest, bog forest, bog woodland, and blanket bog). Boxes represent the second and third quartile ranges, and the centreline is the median.

have an average point density of 2 points·m^{-2} with an average vertical accuracy of 15 cm. A digital terrain surface was generated from classified ground returns using triangular irregular network interpolation and rasterized at a spatial resolution of 1.0 m. The terrain model was used to derive elevation, slope, and aspect as well as to normalize non-ground LiDAR returns to height above ground surface (Gillin et al., 2015). LiDAR data were processed using the FUSION software (version 3.5) (McGaughey, 2015). To compare differences in fire effects to vegetation with LiDAR we used vegetation metrics such as return height percentiles, percent returns above 1 m, average height, canopy relief ratio $[(h_{mean} - h_{min})/(h_{max} - h_{min})]$, and topographical data (Streutker and Glenn, 2006). LiDAR vegetation metrics were calculated for every plot in the study area on 400 m^2 circular plots centred on the plot centre coordinates (n = 70) (Fig. 1).

2.5. Statistical analyses

We used a nested analysis of variance (ANOVA) within the four vegetation types to compare differences in stand composition and structure between burned and unburned plots using the linear and non-linear mixed-effects model package (‘nlme’) in R statistical software (R Development Core Team, 2016; Pinheiro et al., 2017). The site type (burned and unburned plots) represents a random factor at the top of the hierarchy and the sample type (four vegetation types) is the random nesting factor. Including sub-replication (the four vegetation types) in our hierarchical design reduces the unexplained variation and increases the power of the test for the main treatment effect (fire activity). Because our design was not balanced, it was best modelled using a linear mixed- effects model. The data were aggregated and the linear mixed effects model was fit. The variance components of each random effect were assessed to verify the impacts of site and forest type. We calculated the 95% confidence intervals of the random effects (based on Markov chain Monte Carlo sampling) following the methods of Logan (2010). Detailed statistical analyses and model validation are provided in Appendix B: Table B1.

3. Results

3.1. Ecological field data

Our analyses revealed significant differences in forest stand metrics between burned and unburned plots. Trees in burned plots were taller compared to unburned plots with the same vegetation types (*nested analysis of variance*: $F = 14.788$, *d.f.* = 1, $P < 0.0001$; Fig. 2a). Burned plots were also significantly younger than unburned plots in dbh classes > 7.5 cm (*nested analysis of variance:* $F = 279.52$, *d.f.* = 1, $P < 0.001$; Fig. 2b). Only 16% of trees in burned plots were old growth (> 250 years) compared to 58% of trees in unburned plots (Fig. 3; Appendix B: Table B2). Unburned vegetation plots had 132% more stems > 7.5 cm dbh per hectare compared to burned plots (Table 1).

We found no significant difference between dbh in burned and unburned plots across the four forest types (*nested analysis of variance*: $F = 0.3926$, *d.f.* = 1, $P = 0.531$; Appendix A: Fig. A2). Six conifer species (western redcedar, yellow-cedar, western hemlock, shore pine, Sitka spruce, and mountain hemlock) were present in three of the four assessed dbh classes in both burned and unburned plots (Table 1). Sitka spruce and mountain hemlock were not present in the < 7.5 cm dbh class in unburned plots (Table 1).

Regenerating seedlings and saplings < 7.5 cm dbh sampled from subplots located within burned plots were significantly smaller when compared to unburned plots (*nested analysis of variance:* $F = 218.67$, *d.f.* = 1, $P < 0.001$; Fig. 2c). The average combined height of seedlings

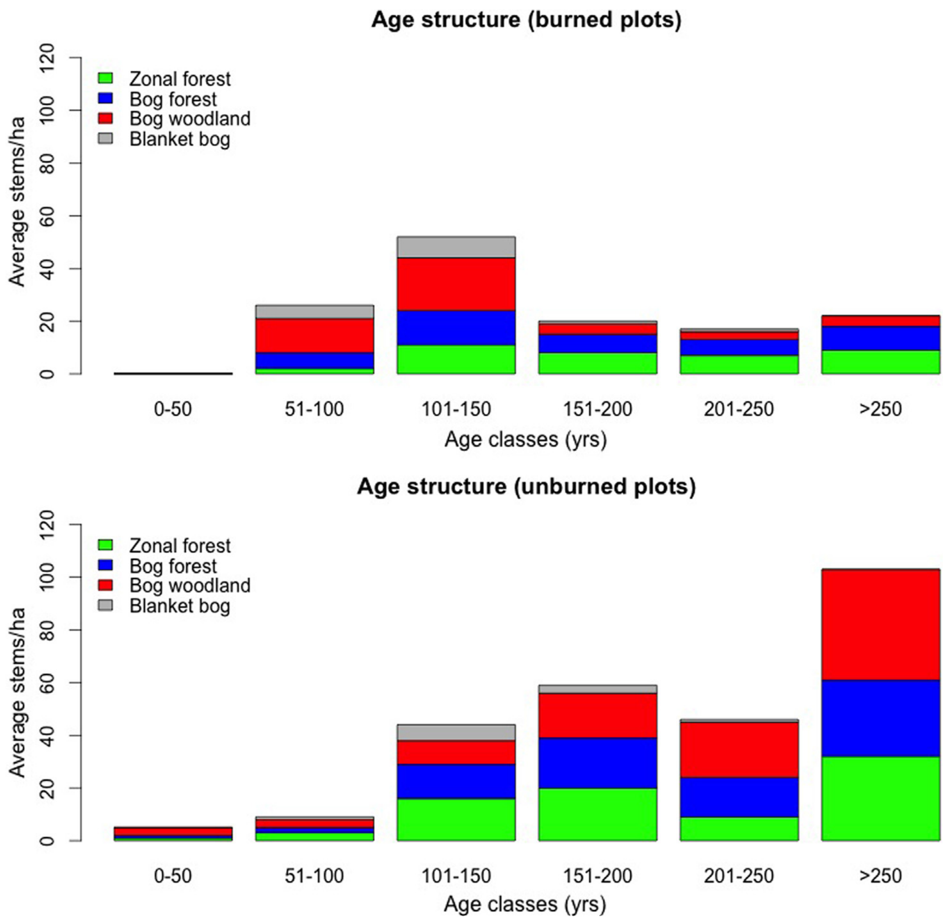

Fig. 3. Six age class distributions are described for the four vegetation types in the study area: zonal forest (green), bog forest (blue), bog woodland (red), and blanket bog (gray) in 27 burned plots (upper panel) and 11 unburned plots (lower panel) with no aboveground evidence of fire activity. The average number of stems per hectare is explained on the y-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and saplings was 23 cm in burned plots compared to 53 cm in unburned plots. Seedlings and saplings in burned plots were also significantly younger (*nested analysis of variance:* $F = 211.72$, *d.f.* $= 1$, $P < 0.001$; Fig. 2d). The average age of seedlings and saplings in burned plots was 12 years compared to 43 years in unburned plots.

Dendrochronological reconstructions of tree ages and post-fire cohorts confirm that surviving trees in burned plots persisted at densities of approximately 75 trees per hectare from 1650 to 1893 (Fig. 4). Sixty-five percent of burned plots contained fire-scarred trees > 400 years and of these, 20 individuals exceeded 1000 years and had survived as many as 16 low- and mixed-severity ground fires (Fig. 4; Appendix B: Table B3). Burned plots contained fire legacies, such as shade tolerant post-fire cohorts dominated by western hemlock, and pulses of shore pine recruitment (Fig. 3). These plots comprised old growth trees (> 250 years) with patches of even-aged forest stands compared to unburned plots, which contained three times the amount of old growth trees (Fig. 3; Appendix B: Table B3).

3.2. LiDAR data

LiDAR confirmed that trees in burned plots were significantly taller than trees in unburned plots based on median and 95th percentile height (*nested analysis of variance*: $F = 7.809$, *d.f.* $= 1$, $P = 0.006$; Fig. 5a). Canopy cover, measured by LiDAR as the proportion of returns above 1 m was also lower in burned plots compared to unburned plots (*nested analysis of variance*: $F = 7.86$, *d.f.* $= 1$, $P = 0.008$; Fig. 5b). Canopy relief ratio, an indicator of canopy complexity, shows that burned plots had a greater spread in vertical biomass than unburned plots (*nested analysis of variance*: $F = 5.23$, *d.f.* $= 1$, $P = 0.028$; Fig. 5c).

4. Discussion

In this study, we examine the legacies of historic fire activity on the height, density, diversity, and structure of forests in our temperate rainforest study region more than one hundred years after the last fire. Although historically burned plots had fewer trees (Fig. 3; Appendix B: Table B2), we found these plots contained higher conifer diversity than unburned plots (Table 1). Trees in burned plots were also taller and younger compared to trees in plots that have not burned in at least 1000 years (Fig. 2; Appendix B: Table B2). The persistence of ecological legacies over long temporal and across broad spatial scales suggests that historic fire disturbances continue to affect present day forest structure and composition and will likely shape responses to future disturbances (Peterson, 2002; Johnstone et al., 2016). Our multi-scale approach examining the effects of historic fire to seedlings, saplings, and mature trees supports our hypothesis that burned plots contain younger and taller trees with lower stem density (Fig. 2; Appendix A: Fig. A3). However, trees in burned plots did not contain on average larger dbh as hypothesized (Appendix 1: Fig. A2).

The ability of researchers to detect fire legacies depends on the presence of fire-scarred trees and post-fire cohorts as well as the capacity of surviving mature individuals to act as seed sources between fire events (Agee, 1993). Seedlings can also germinate from the soil seed bank, or regenerate from germinating individuals that survived the fire (Bartels et al., 2016). The type of regeneration plays an important role in the timing and recovery of the disturbed forest and in structural development patterns (Oliver and Larson, 1996). Recovery is faster following low-severity fire disturbances that cause minimal impacts to vegetation, roots, and soil substrates and leave much of the existing forest structure intact (Agee, 1993; Foster et al., 1998). Old growth stands with varying fire histories continue to undergo compositional

Table 1
The density of trees, saplings, and seedlings per hectare were binned into four diameter at breast height (dbh) classes (1.5–7.5, 7.6–20, 20.1–40, and > 40.1) for each of the six species, which characterize the four dominant vegetation types in the study area in (A) 27 burned plots and, (B) 11 unburned plots. The symbol (–) indicates that the species was not present.

dbh class and vegetation type	Western redcedar	Yellow-cedar	Western hemlock	Sitka spruce	Shore pine	Mountain hemlock
(A) Burned plots (n = 27)						
Density of trees/ha > 40.1 dbh						
Zonal forest	120	30	15	20	–	–
Bog forest	87	34	–	–	17	–
Bog woodland	35	10	3	–	–	–
Blanket bog	–	–	–	–	–	–
Density of trees/ha 20.1–40 dbh						
Zonal forest	150	50	100	5	35	30
Bog forest	180	232	76	–	118	11
Bog woodland	33	25	–	–	95	5
Blanket bog	7	4	–	–	–	–
Density of trees/ha 7.6–20 dbh						
Zonal forest	120	45	275	5	–	–
Bog forest	148	100	123	3	126	11
Bog woodland	137	190	3	3	478	15
Blanket bog	38	34	–	–	260	–
Density of trees/ha 1.5–7.5 dbh						
Zonal forest	39,166	2600	25,000	500	4500	–
Bog forest	29,500	6000	21,000	–	4000	1000
Bog woodland	35,000	6500	5000	–	27,500	1000
Blanket bog	11,000	6000	2500	–	21,500	500
(B) Unburned plots (n = 11)						
Density of trees/ha > 40.1 dbh						
Zonal forest	225	50	–	50	–	–
Bog forest	75	25	–	–	–	–
Bog woodland	25	–	–	–	–	–
Blanket bog	–	–	–	–	–	–
Density of trees/ha 20.1–40 dbh						
Zonal forest	275	300	100	–	25	–
Bog forest	325	21	100	–	200	25
Bog woodland	125	100	25	–	50	25
Blanket bog	25	25	–	–	–	–
Density of trees/ha 7.6–20 dbh						
Zonal forest	275	100	550	–	25	–
Bog forest	400	125	125	–	350	25
Bog woodland	475	675	200	–	700	50
Blanket bog	25	–	–	–	213	–
Density of trees/ha 1.5–7.5 dbh						
Zonal forest	14,500	3000	21,000	–	–	–
Bog forest	24,500	10,000	6500	–	2500	–
Bog woodland	54,000	29,500	2000	–	4500	–
Blanket bog	9000	5000	1000	–	500	–

change related to stand histories and current population interactions (Tepley et al., 2013). Direct fire effects include changes to stand density, size structure and establishment rates, and the effects of local competition on growth and mortality (Foster et al., 1998).

In zonal and bog forest vegetation types, the majority of mature trees survived repeated low-severity ground fires and remained seed sources between fire events (Fig. 4). Our data confirm that historic fire events occurred on average every 39 years (Hoffman et al., 2016b). This return interval suggests that subsequent fires would have negatively affected the survival of regenerating trees and their ability to sufficiently mature to produce seeds between fire events (Fig. 2c and 2d). Therefore, older surviving individuals likely remained an important seed source and may explain why there has been very little change in species composition during the last six centuries (Table 1; Fig. 4). In bog woodland and blanket bog vegetation types, regeneration occurred via surviving mature trees and through vegetative regeneration by root suckering, stem sprouting, and layering. Vegetative regeneration is more common when fewer seed sources (mature trees) are present, and can be favourable as vegetation regeneration does not require mineral soil substrates for germination and less time is required for regeneration (Bartels et al., 2016).

Repeat low-severity ground fires likely reduced understory tree densities and decreased the amount of available fuel in burned plots (Figs. 4 and 5a). Saplings (< 7.5 cm dbh) and seedlings (< 15 cm) in burned plots were significantly younger than in unburned plots (12 compared to 43 years) indicating that a denser canopy and increased competition for resources in unburned plots may have resulted in the suppression of understory trees (Figs. 2d and 5b). The majority of understory trees in unburned plots were comprised of western hemlock, which can remain suppressed in the understory canopy for decades until disturbances such as tree gap formation and replacement (Fig. 3; Bartemucci et al., 2002; Lertzman et al., 2002). Although western redcedar, yellow-cedar, and western hemlock were common regenerating species in both burned and unburned plots, less shade tolerant species such as Sitka spruce and mountain hemlock were not present when we examined saplings and seedlings in unburned plots (Table 1b; Appendix A: Fig. A3). These species were found in higher densities in burned plots, which were less dense and had a more open canopy structure, which provided more available light for regeneration (Table 1b; Fig. 4).

We hypothesized that the dbh of trees in burned plots would be on average larger than the dbh of trees in unburned plots as a result of decreased competition for light, below-ground nutrients, and space. This pattern was not apparent in our results and we suggest this finding may be explained by the presence of slow-growing tree species (many individuals exceed 1000 years) and nutrient-poor soil conditions (Appendix A: Fig. A2). Therefore, the legacy effects of low-severity fires on temperate rainforest stand productivity may be slower than previously estimated. Significant knowledge gaps exist in our understanding of the long-term effects of fire on the growth and productivity of temperate rainforest tree species.

Tree seedlings are less likely to successfully establish and survive when repeat fire disturbances are compounded by climate variability (Kemp et al., 2016). Therefore, differences in stand densities may be a product of fire history and climate combined (Stevens-Rumann and Morgan, 2016). Although we accounted for differences in underlying vegetation patterns, terrain, and site characteristics in the four forest types, a warming climate in the 20th century may have played an important role in forest regeneration and stand dynamics following the 1893 fire (Tepley et al., 2016). Thus, examining differences through time by looking at multiple years since the most recent fire is important, as differences between burned and unburned plots may be explained, in part, by climate variability (Tepley et al., 2013). A comprehensive analysis of tree density along with tree seedling establishment through time with potential climate and topographic correlations would improve our understanding of the mechanisms of recovery following historic fires (Tepley et al., 2016). Unfortunately, this was not possible in our study because too much time has elapsed since the most recent fire.

LiDAR has the ability to represent complex vertical structures and ground surfaces with high precision (Bartels et al., 2016). Unfortunately, the accuracy and precision of LiDAR decreases when it is

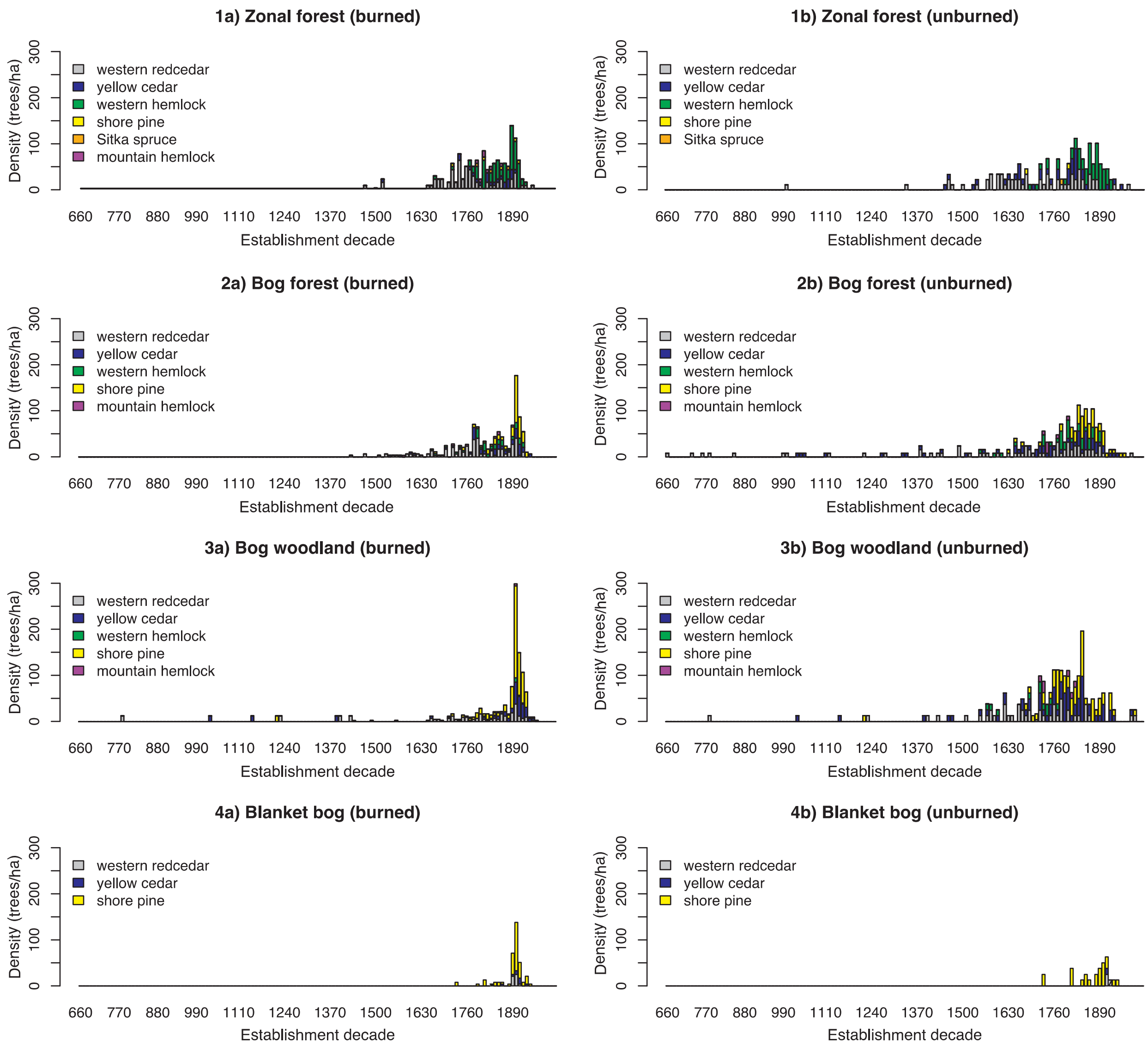

Fig. 4. The 1353 year record (spanning 660–2013) of density of trees per hectare binned by decade of establishment in burned verses unburned plots across four vegetation types (zonal forest, bog forest, bog woodland, and blanket bog) in the study area. Species are western redcedar (gray), yellow-cedar (blue), western hemlock (green), shore pine (yellow), Sitka spruce (orange), and mountain hemlock (purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

applied to heterogeneous landscapes that are characterized by patchy vegetation and high structural variability (Swetnam et al., 2011). In relatively homogenous forest stands characterized by high-severity stand-replacing fires, canopy cover often recovers quickly, while canopy height takes several decades to return to pre-fire conditions (Bolton et al., 2017; McCarley et al., 2017). Forest metrics derived from LiDAR detected differences in canopy height and complexity in burned plots 124 years after the most recent fire event (Fig. 4). We were able to detect fire legacies in our study area with LiDAR because centuries of repeat low-severity fires continue to influence the present day stand structure and affect regeneration processes resulting in increased canopy complexity and lower canopy cover (Fig. 4).

The capacity of remotely sensed data to characterize post-fire disturbances is increasing as data sources are becoming more widely available and less costly (Swetnam et al., 2015; Gordon et al., 2017). How ecological communities change following fire disturbance is important for ongoing forest management and our understanding of old growth forests facing a rapidly changing climate (Bartels et al., 2016). While remote sensing techniques such as LiDAR are able to characterize broad geographical areas, plot-level measurements remain important calibration and validation tools (Bartels et al., 2016) and may identify processes that can be overlooked by remote sensing methods (McCarley et al., 2017). For example, we utilized 32 additional ground-truthed plots sampled with LiDAR to assess the feasibility of creating a predictive model to examine the potential locations of historic fire activity in forests outside of our study area. Unfortunately, we found that the natural variability in temperate rainforest structure surpassed the effect of fire legacies, which impeded the predictive capabilities of a landscape-scale model. Therefore, we find that the spatial extent to which our results can be applied is at the local scale (Central Coast hypermaritime region) and our results confirm that plot-level measurements are required to validate historic fire activity in our study area.

Remote sensing techniques are often employed to detect and predict the locations of recent fire disturbances in boreal, arid, and temperate forest ecosystems (White et al., 1996; Díaz-Delgado et al., 2003; Bolton et al., 2017). We find these modeling techniques do not readily detect long-term fire legacies in our high biomass, high-latitude coastal temperate rainforest study area, despite similarities in the structure of historically burned forests plots, with drier, inland forests dominated by fire-adapted vegetation, post-fire cohorts, and open canopies (Stevens-

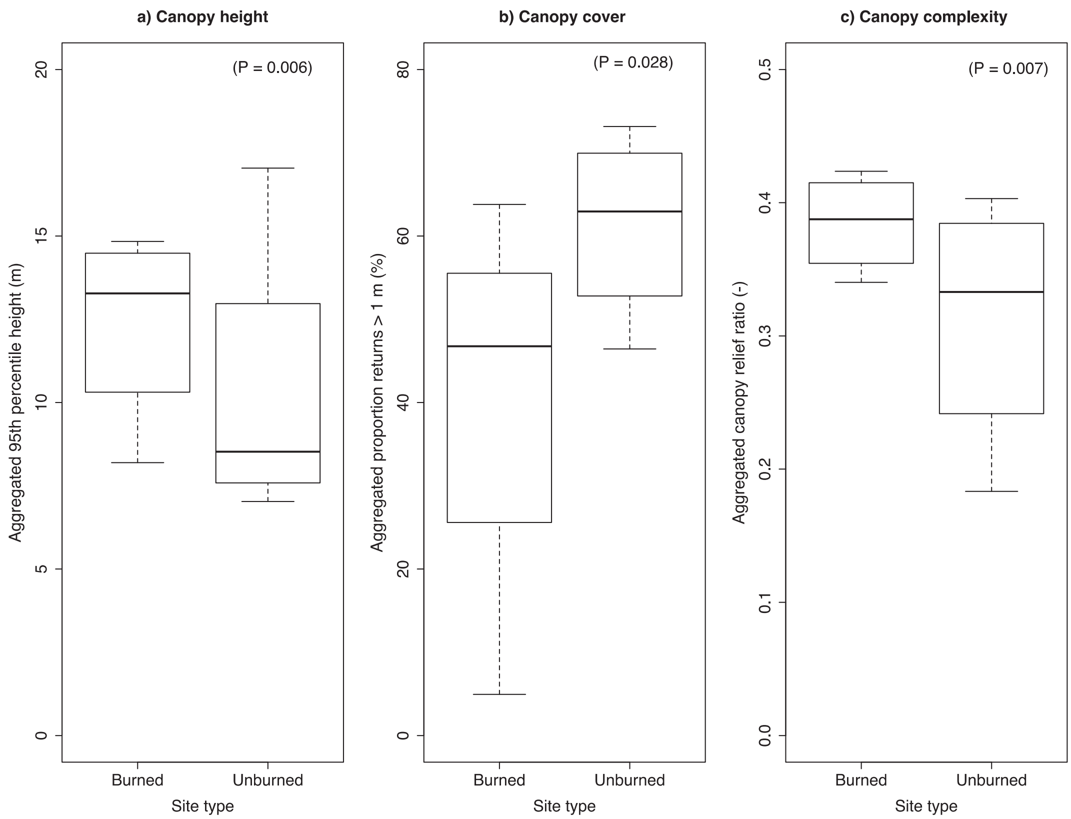

Fig. 5. The results of the two factor model nested analysis of variance (ANOVA) with unequal sample sizes. Box and whisker plots describe differences in airborne light detection and ranging (LiDAR) measurements for (a) canopy height, (b) canopy cover, and (c) canopy complexity between burned and unburned plots aggregated across four vegetation types (zonal forest, bog forest, bog woodland, and blanket bog). Boxes represent the second and third quartile ranges, and the centreline is the median.

Rumann and Morgan, 2016). This finding suggests that more research and broader comparisons are required to understand low- and mixed-severity fire regimes across British Columbia's diverse forest types (Heyerdahl et al., 2012). Our findings suggest the importance of integrating plot-level measurements with remote sensing techniques to capture the full range of variability of a landscape or region and reliably inform site-specific forest management (McKenzie and Kennedy, 2011; Swetnam et al., 2015; McCarley et al., 2017).

4.1. Management implications

Very little is known of fire disturbances in coastal temperate rainforests, and analyses of contemporary fire activity often do not consider the disruption of traditional fire management systems following the arrival of European colonists in North America (Ryan et al., 2013). In most of coastal British Columbia, fire activity was altered through widespread logging in the 1900s, grazing in the 1970s, and fire suppression beginning in the 1920s (Ryan et al., 2013; Turner et al., 2013). Fire suppression policies also directly impacted First Nations and their traditional fire-management systems (Turner et al., 2013). Despite the lack of empirical data describing historic fire activity, the popular and widely accepted view of fire disturbance in high-latitude coastal temperate rainforests emphasizes infrequent, high-severity stand-replacing fires occurring at centennial or millennial scales (B.C. Forest Practices, 1995; Daniels and Gray, 2006). Stand-replacing fire models have been assumed due to the availability of biomass and volatility of fuels, which characterize western redcedar and western hemlock dominated forests (Agee, 1993; Daniels and Gray, 2006; Whitlock et al., 2010).

Until recently, no fire histories have been reconstructed with fire scars in British Columbia high-latitude coastal temperate rainforests, and fire records based on post-fire cohorts are limited to drier, Douglas-fir (*Pseudotsuga menziesii*) dominated sites (Gavin et al., 2003). Our fire history reconstruction suggests that low- and mixed-severity fires were once more frequent and occurred on average every 39 years prior to the reduction of activity of First Nations in their territories in the late 19th century (Hoffman et al., 2016b; Appendix A: Table 1). Applying stand-replacing models of fire activity with no direct empirical evidence in this region could limit our understanding of the effects of climate change on forest development and greatly underrepresent the diversity of old growth forest structures and development pathways in this ecosystem (Tepley and Veblen, 2015). Current reforestation guidelines in British Columbia hypermaritime forests (CWHvh2) promote diverse and dense plantations while encouraging patches of early seral vegetation (B.C. Forest Practices, 1995). While these practices are in line with stand-replacing fire disturbances, they do not represent the low- and mixed-severity ground fires, which historically characterized the region.

5. Conclusions

Our comparative analysis of LiDAR remote sensing and plot-level measurements in burned and unburned vegetation plots confirm that legacies of low-severity fires continue to shape structural and regeneration patterns in present day forests (Table 1). Although it has been more than 120 years since the most recent fire event on Hecate Island, burned vegetation plots were distinct in their composition and structure when compared to unburned plots. As remotely derived images become increasingly available, ecological field sampling and plot-level measurements remain necessary to accurately compare and validate vegetation metrics (Swetnam et al., 2015). We find that LiDAR is an important tool for mapping and characterizing coastal temperate rainforest structure and improves our understanding of the spatial components of fire. LiDAR can detect differences in canopy complexity, stand density, and stand height between burned and unburned plots, but ground-truthing is still necessary to verify species composition, and the severity and temporal properties of historic fire disturbances. Our study suggests that fire history and the development and maintenance of old growth forests in heterogeneous landscapes such as British Columbia's old growth coastal temperate rainforests are more complex than previously estimated.

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Author contributions

KMH conceived the manuscript ideas. KMH, AJT and WN collected and analyzed the data with assistance from BMS. KMH, AJT, WN and BMS drafted the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.04.020.

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