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Ecological legacies of anthropogenic burning in a British Columbia coastal temperate rain forest

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Abstract

Aim: Few long-term fire histories have been reconstructed in coastal temperate rain forests, and little is known regarding the spatial and temporal characteristics of lightning and human ignitions. We use a multidisciplinary approach to assess the impact, scale and ecological legacies of historic fires.

Location: We focus on perhumid temperate rain forests located on the central coast of British Columbia, Canada.

Methods: We reconstructed 700 years of temporal and spatial aspects of fire activity with 30 plots on Hecate Island using fire scars and forest-stand establishment. We then conducted a paired study of 20 former indigenous habitation and control sites on 15 islands to relate fire activity to patterns of human settlement. We mapped 15 years of lightning strike densities and use mixed-effects modelling to assess whether fire activity predicted the distribution and abundance of traditional plants.

Results: Sixteen low- and mixed-severity fires were recorded from 1376 to 1893. The abundance of traditional plants and the density of western redcedar trees were best predicted by the location of former habitation sites and shorter mean fire intervals. Lightning is too rare to explain the pattern of fire activity in the study area. No fire activity was detected after 1893, coinciding with the relocation of indigenous groups from the study area.

Main conclusions: Fire was strongly associated with former indigenous habitation sites during the periods of occupation. People likely utilized fire as a tool for resource management to influence the densities of specific plants by creating mosaics of vegetation in different stages of succession. By assessing the ecological impacts of historic fire events, we gain a better understanding of the abrupt changes that occurred in the 20th century. Our ability to understand present-day temperate rain forest ecosystems may be compromised if we underestimate the role of humans in driving historic fire activity.

KEYWORDS
anthropogenic burning, British Columbia, coastal temperate rain forest, ecological legacies, fire history, human-driven fire activity

1 | INTRODUCTION

Fire is one of the most important mechanisms driving landscape-scale ecological dynamics, plant community structure and soil properties (Bowman et al., 2009). Humans have altered fire regimes for millennia in many different ecosystems by igniting and suppressing fires and modifying fuel composition and structure (Pausas & Keeley, 2009). Because fire is both a stochastic, natural process and an intentional, cultural process, there is much debate regarding the relative importance of lightning versus human ignitions (Krasnow, Fry, & Stephens, 2016; Marlon et al., 2012; Rolstad, Blanck, & Storaunet, 2017; Ryan, Knapp, & Varner, 2013). Climate is a primary driver of fire activity at regional scales, shaping the composition and distribution of vegetation and governing weather conditions that promote fire initiation and spread (Krawchuk & Moritz, 2011). At broad scales, human influences are considered secondary to climate because their effects are geographically localized (Whitlock et al., 2015), and the relative roles of humans and climate are difficult to discriminate and generalize (Ryan et al., 2013). The historic and contemporary dynamics of fire activity in fire-prone landscapes have been well studied. However, current fire-history methods which heavily rely on fire-scar records alone are likely inadequate to decouple natural and anthropogenic contributions to historic fire activity in temperate rain forests (Bowman et al., 2011; McWethy et al., 2013). Globally, coastal temperate rain forests contain ample biomass for burning, but are considered both climate- and ignition-limited systems due to high year-round fuel moisture levels (Bowman et al., 2009; Power et al., 2008; Whitlock et al., 2015). Reconstructions of forest stand establishment following historic fire events and improved data on indigenous fire-management systems may provide a greater understanding of fire activity in coastal temperate rain forests.

Perhumid or high-latitude (>50°N) coastal temperate rain forests extend from the northern tip of Vancouver Island to the panhandle of Alaska (Dellasala et al., 2011). These forests are the wettest variant of the temperate rain forest biome and are considered to have low natural resilience to fire (Dellasala et al., 2011). In these forests, fuel moisture levels rarely drop to the point of ignition and a thick layer of fog often blankets the coastline even in the summer months (Daniels & Gray, 2006). Despite the seemingly unsuitable conditions for fire, recent research suggests that short-term summer drought does occur (Hoffman, Gavin, & Starzomski, 2016) and that fire has been an important component of some forests in this region for millennia, with associated impacts on the abundance, diversity and availability of plant resources (Trant et al., 2016).

Anthropogenic burning refers to both intentional and accidental ignitions by people (Guyette, Muzika, & Dey, 2002). In this article, we consider intentional burning as the practice of periodic burning of landscapes or particular sites by indigenous peoples over time to achieve specific management goals (Turner, Deur, & Lepofsky, 2013). Although oral histories of intentional burning are well documented in southern and interior areas of British Columbia (Turner, 2014), we know little regarding how various cultural groups utilized fire on the central coast of British Columbia and consequently how differing management practices affected ecosystem patterns and processes. Reconstructing the frequency and extent of intentional burning is challenging because many fire-management practices have subtle ecological legacies and many recollections of burning have faded from memory (Lepofsky et al., 2005). Reconstructions are rendered more difficult by the arrival of Europeans on the coast of British Columbia in the late 18th and 19th centuries which in many regions resulted in cultural suppression and erased legacies of indigenous land-use practices through logging, agriculture and livestock grazing (Turner et al., 2013).

The rarity of summer lightning (Lertzman et al., 2002), availability of biomass for burning (Daniels & Gray, 2006) and a >13,000 year history of human habitation (McLaren, Rahemtulla, Gitla (White, E.) & Fedje, 2015) make the central coast of British Columbia an ideal location to examine historic fire activity. The goal of this study is to use a weight-of-evidence approach combining quantitative and qualitative data to improve our understanding of the temporal and spatial attributes of historic fire activity, the probability of lightning and human ignitions and how fire impacted landscape patterns and processes (Lepofsky, Heyerdahl, Lertzman, Schaepe, & Mierendorf, 2003). We utilized multiple lines of evidence to test three hypotheses: (1) fires were natural (lightning caused), (2) fires were human (accidental ignitions) and (3) fires were human (intentional ignitions). We predicted the spatial and temporal attributes, severity and cyclical patterns of historic fire activity along with changes to fire activity in the 20th century. Our hypotheses, predictions for each test and support for each model are described in Table 1. Further direct and indirect ethnobotanical evidence of anthropogenic burning is outlined in the Supporting Information (Tables S1.1; S1.2).

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is composed of a 2,000 km^2 island group on the coastal margin of central British Columbia, Canada (Figure 1). This region is characterized by a temperate climate with year-round cool temperatures (average annual *c.* 7°C, average summer *c.* 12°C) and annual rainfall that locally may exceed 4,000 mm (Banner, LePage, Moran, & Groot, 2005). The Pacific Ocean moderates temperatures throughout the year and the British Columbia Coast Mountains protect the islands on the outer coast from cold winter and hot summer continental air masses (Dellasala et al., 2011). Located within the very wet hypermaritime variant of the Coastal Western Hemlock biogeoclimatic zone, this region is characterized by low rates of evapotranspiration and soils that remain saturated throughout the year (Meidinger & Pojar, 1991).

2.2 | Vegetation

Productive forests are dominated by western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), with lesser amounts of yellow-cedar (*Cupressus nootkatensis*

TABLE 1 Three hypotheses were tested using a weight-of-evidence approach to infer the spatial and temporal attributes of historic fire activity and to assess whether fire ignitions were human or lightning caused. The hypotheses and predictions for each test are detailed. The bold text indicates whether the prediction is consistent with lightning or human ignitions. Multiple lines of evidence are consistent with intentional ignitions by humans on the central coast of British Columbia, Canada

Hypotheses	Ignition source	Prediction: frequency	Prediction: intensity	Prediction: size	Prediction: spatial attributes	Prediction: temporal attributes	Prediction: forest age	Prediction: plant community composition	Prediction: 20th century changes	Findings
1. Non-human ignitions	Lightning	Rare, centennial/millennial scales (Lertzman et al., 2002) **Not consistent**	Mixed- and high-severity (Agee, 1993) **Not consistent**	Large, patchy fires (Agee, 1993) **Not consistent**	High and mid elevations, rocky outcrops (Burrows et al., 2002) **Not consistent**	Long fire return intervals (Lertzman et al., 2002) **Not consistent**	Old growth >250 years (Daniels & Gray, 2006) **Not consistent**	Natural pattern in distribution of food plants **Not consistent**	No changes to fire activity (Daniels & Gray, 2006) **Not consistent**	***Evidence is not consistent*** with this hypothesis
2. Human ignitions (accidental)	Human	Less frequent decadal/centennial scales (Turner, 1999) **Not consistent**	Low- and mixed-severity (Turner, 1999, 2014) **Consistent**	Small fires (<3 ha) (Hoffman, Gavin, & Starzomski, 2016; Turner, 1999) **Consistent**	Fires located within former habitation sites **Consistent**	No cyclical pattern **Not consistent**	Old growth, younger cohorts near former habitation sites **Consistent**	Natural pattern in distribution of food plants **Not consistent**	No fire ignitions in 20th century (Hoffman, Gavin, & Starzomski, 2016) **Consistent**	***Some of the evidence is consistent*** with this hypothesis
3. Human ignitions (intentional)	Human	Frequent interannual/decadal scales (Lepofsky et al., 2003; Turner, 1999, 2014) **Consistent**	Low- and mixed-severity (Turner, 1999, 2014) **Consistent**	Small fires (<3 ha) (Hoffman, Gavin, & Starzomski, 2016; Turner, 1999) **Consistent**	Fires located on the edges of former habitation sites (Hoffman, Gavin, Lertzman, Smith, & Starzomski, 2016; Hoffman, Gavin, & Starzomski, 2016; Turner, 1999; Wray, 2009) **Consistent**	Cyclical pattern (~19 years) in plots surrounding former habitation sites (Turner, 1999) **Consistent**	All aged stands, open areas and evidence of even-aged cohorts from previous fires **Consistent**	Food plants associated with burned areas in higher densities (Turner, 1999, 2014) **Consistent**	No fire ignitions in 20th century (Lepofsky et al., 2003) **Consistent**	***Evidence is consistent*** with this hypothesis
Supporting data	Real-time lightning data, fire locations, fire timing	Fire-history analyses, fire scars (N = 99), post-fire cohorts (from 4,000 tree cores)	Fire-scarred trees (N = 99), fire maps	Point locations of fire scars (PFI), fire maps	Fire scars (N = 99), post-fire cohorts (from 4,000 tree cores), lightning strike data (15 years), transects (n = 20), oral histories in similar systems	Fire scars (N = 99), post-fire cohorts (from 4,000 tree cores)	Fire-history plots (N = 30), transects (N = 20)	Plant community and composition plots (N = 30), transects (N = 20), oral histories in nearby and similar ecosystems	Fire scars, fire maps, time since most recent fire, historical data	Ethno-historical accounts of the season and timing of fires and the sites selected for burning are ***required***

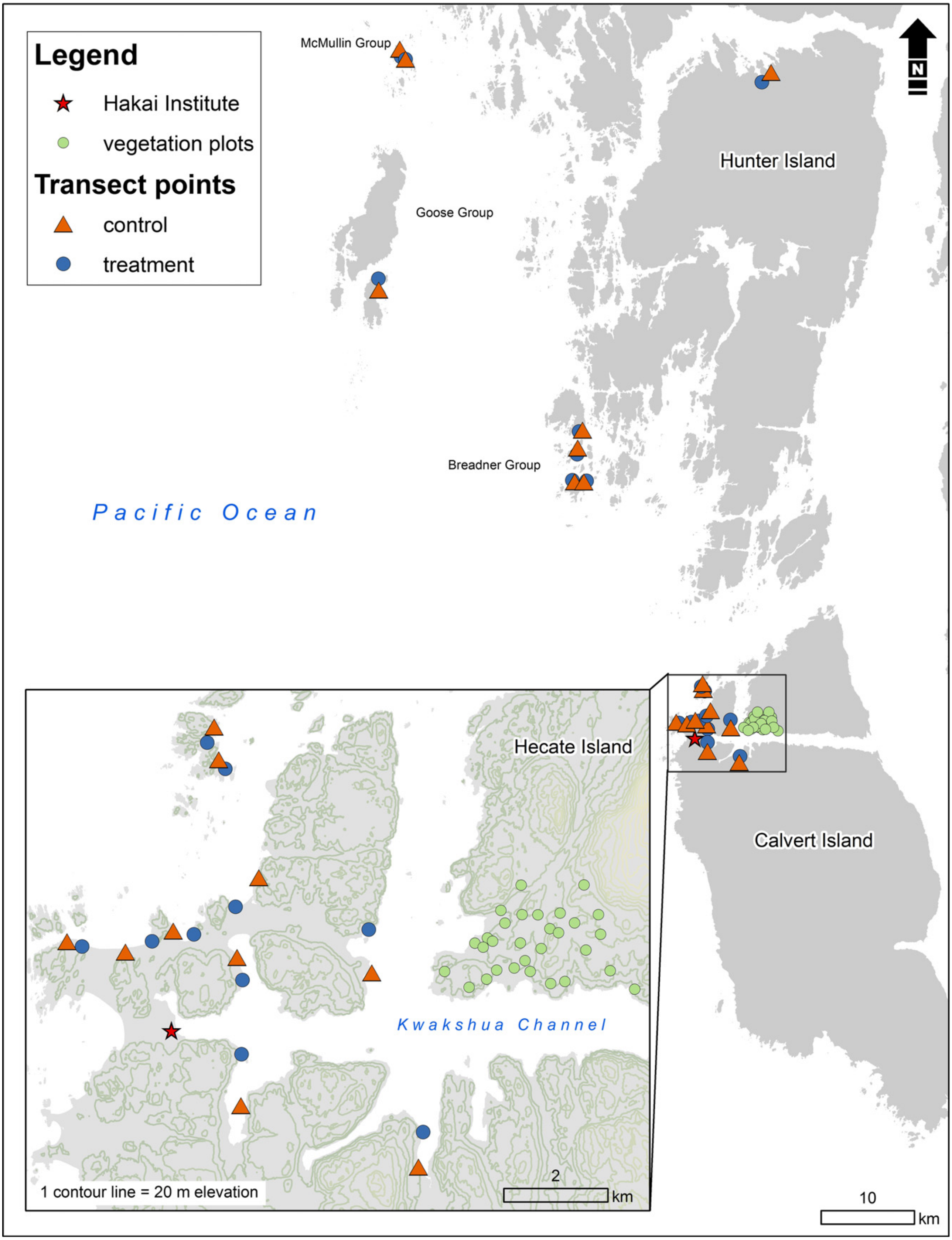

FIGURE 1 The location of the 2,000 km^2 study area on the central coast of British Columbia, Canada. Triangles and circles represent the locations of the 20 transects (former habitation and control sites) used to assess the association between fire activity and humans. The star symbol is the location of the Hakai Institute. The map inset provides the location of the 30 fire-history plots on Hecate Island

[D.Don] Farjon & Harder) and Sitka spruce (*Picea sitchensis* [Bong.] Carr.). However, productive forests are restricted to steeper slopes or riparian and nearshore areas with nutrient-rich and moderately drained soils. This is in contrast to the majority of vegetation types in the study area, which exhibit stunted growth forms as a result of prolonged saturation and acidic soil conditions (Banner et al., 2005). Less productive vegetation types include bog forests and bog woodlands, which grow in moderate and poorly drained soils on rolling terrain and form a patchy mosaic of heterogeneous woodlands dominated by cedars, western hemlock and shore pine (*Pinus contorta* var. *contorta* Douglas ex Louden). Blanket bog vegetation types are located on subdued terrain and contain nutrient-poor soils with shrubby, short-statured vegetation (Banner et al., 2005).

2.3 | Human history

Compared with other coastal regions of British Columbia, sea levels in the study area have been relatively stable (±2 m) throughout the Holocene period and cultural sites remain well preserved on the landscape (McLaren et al., 2014). The combination of sea-level stability, a mild climate and abundant terrestrial and marine resources supported continuous settlement in the region for at least the last 13,000 years (McLaren et al., 2015). The study area includes numerous former indigenous habitation sites with an accumulation of shell-midden deposits and nearshore features including clam gardens, fish traps and culturally modified trees (CMTs) (McLaren et al., 2015; Trant et al., 2016). There are no ethnographic accounts of anthropogenic burning in the study area, but elders in the nearby community of Waglisla (Bella Bella) describe older generations repeatedly burning hillslopes and interior mountain sites to increase the abundance of blueberries (*Vaccinium* spp.) (Turner, 2014). There are also oral histories of burning off vegetation on small islands in nearby Haida Gwaii to establish ownership and to increase the productivity of food-producing plants (Turner, 1999). Although indigenous seasonal-resource gathering continues in the study area, habitation sites have not been occupied since at least the end of the 19th century (McLaren et al., 2015). The majority of the landscape has not been logged, potentially preserving ecological legacies of long-term indigenous land-use practices.

2.4 | Fire-history reconstruction: Hecate Island

We completed a fire-history case study in a historic 287 ha burn located on Hecate Island (N51°39 Latitude, W128°04 Longitude) (Figure 1; see also Hoffman, Gavin, & Starzomski, 2016). This site was chosen for a detailed fire history because it contained abundant, rot resistant and long-lived (>1,000 years) fire-scarred trees. Fire-scarred trees are rare in perhumid coastal temperate rain forests due to long fire-free intervals (Lertzman et al., 2002), intolerance to fire of local tree species and high rates of wood decomposition (Daniels & Gray, 2006). To reconstruct historic fire activity and identify contemporary vegetation patterns associated with anthropogenic burning, we sampled fire scars, forest-stand establishment and described plant species richness and abundance from 30 plots (11.28 m radius [0.04 ha]) selected using a stratified random sampling design representing the range of elevations, aspects and dominant vegetation types in the area (Figure 1).

In the 1-hectare area surrounding every plot, we used a chainsaw to remove partial wedge sections of fire scars from the bases of the oldest sound living trees (determined after coring and measuring) (Arno & Sneck, 1977). We sampled two 5-mm increment cores roughly 1.3 m from the ground from 100 trees in forests located outside of the 287-ha perimeter with no aboveground fire evidence to ensure cross-dating accuracy in the fire-history chronology (Johnson & Gutsell, 1994). In every plot, we removed two 5-mm increment cores from the root collar of every living tree >7.5 cm diameter at breast height (DBH) to determine the year of establishment (Tepley & Veblen, 2015). We used the presence of fire-scarred trees to assess fire severity and assigned post-fire cohorts to the same year as a fire event if they occurred within the 10-year period of a nearby fire scar (Heyerdahl, Brubaker, & Agee, 2001). In the laboratory, cores and wedges were processed using standard dendrochronological techniques (Stokes & Smiley, 1968). Samples were first visually cross-dated 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. We compiled fire scars into a composite chronology and identified fire events as those in which at least two trees had fire scars (Heyerdahl et al., 2001). We calculated point fire intervals (PFI [years between successive fires at plot locations]) and composite mean fire intervals (MFI [years between successive fires anywhere in the study area]) and mapped the spatial and temporal extent of historical fires (Tepley & Veblen, 2015).

We completed vegetation surveys and estimated the percent cover and richness of all living and dead tree, shrub, herbaceous and non-herbaceous species in every plot to assess the potential effects of historic fire activity on present-day plant communities. Specifically, we examined the relationship between fire events and the abundance and composition of traditional plants that were historically utilized for food and medicine (Turner, 2014). A list of all species sampled in the study area and ethnobotanical references of traditional plants associated with historic fire-management systems in British Columbia are provided in the Supporting Information (Table S1.1; S1.2).

Because we expected clustering of the four vegetation types (zonal forest, bog forest, bog woodland and blanket bog) in the data (vegetation types would be more similar within groups than between groups), we analysed the data using a generalized linear mixed-effects model (GLMM) with a Poisson distribution to account for spatial dependencies within sites. We used the "glmmML" and "MuMIn" packages in the computer program R (Barton, 2016; Brostrom, 2013; R Development Core Team, 2016) following the methods of Zuur, Ieno, Walker, Saveliev, and Smith (2009). We analysed the distribution of each response (density of western redcedar trees and percent cover of traditional food plants) with the predictor variables MFI, elevation, aspect, slope, distance to shoreline and distance to former habitation site. We described the relationship between the response and predictor variables using regression coefficients that vary with respect to the random effect (vegetation type). All explanatory variables with high collinearity (variance inflation factor [VIF] >3) were removed and models were compared with Akaike information criterion (AIC_c).

2.5 | Regional fire-history surveys

We sampled belt transects (6 × 30 m long) in a paired design to examine the presence of fire activity in forests surrounding former habitation and control sites (*n* = 20) located on 15 islands throughout the study area (Figure 1). We selected former habitation sites containing established shell midden and archaeological records of occupation throughout the Holocene (McLaren et al., 2014, 2015). These sites were compared to controls that were selected for their similar vegetation structure and site attributes (aspect, slope and elevation), but lacked any aboveground or belowground evidence of shell midden. Controls were either located on separate islands (75%) or several hundred metres away from former habitation sites to limit the potential of previous fires burning through treatment and control transects. The location of transects at each site was randomly assigned based on the size of the nearshore site area, and transects 6 × 30 m long in replicates of three were completed at the present-day forest edge at each former habitation and control site. Thus, sites with wider shorelines would have the three transects spaced further apart, on average, than sites with narrower shorelines. The height and decay class of all trees >15 cm DBH were sampled in transects along with the presence of CMTs, fire scars and coarse woody debris (CWD).

2.6 | Lightning strike densities

We assessed the exact locations of lightning strikes with a peak current >5 Ka (the minimum estimated current strength to promote fire ignition) in the 2,000 km^2 study area for the period 1999–2014 (CLDN, 2016). We acquired the data from the Canadian Lightning Detection Network, which includes real-time strike locations with negative and positive polarity (CLDN, 2016). A log likelihood ratio (G-test) test of independence was performed to assess the association between lightning strike locations with prolonged summer (May–September) dry periods related to instances of low fuel moisture (Krawchuk & Moritz, 2011). Monthly gridded temperature and precipitation data were extracted from ClimateBC (version 5.41) (Wang, Hamann, Spittlehouse, & Murdock, 2012).

3 | RESULTS

3.1 | Fire-history reconstruction: Hecate Island

Sixteen fire events were recorded on 45 partial sections of living fire-scarred trees in the 287-ha fire perimeter located on Hecate Island (Figure 2; Table S1.3). The fire-history chronology spanned the calendar years 1330–2014 (684 years). The first fire event occurred in 1376 and the last and the largest fire event occurred in 1893 when 90% of plots burned in a 287-ha low- and mixed-severity fire (Figure 2). We dated 99 fire scars on 45 trees, the majority of which were recorded on living western redcedar trees. Trees containing fire scars were >400 years at the majority (65%) of plots. We were unable to determine the intra ring position (seasonality) on most samples due to rot and narrowing of tree rings at fire-scar margins. Fire-size estimates inferred from the location of trees bearing fire scars dating the same fire year and the locations of post-fire stand establishment ranged from 0.01 to 287-ha, with a median size of 3-ha (Figure 2). The PFI was 95 years and composite MFI was 39 years (based on a 517-year reconstruction from 1376–1893; Table S1.3). We found no evidence of fire scars, post-fire stand establishment or char on trees after the last recorded fire in 1893.

3.2 | Fire and plant communities

We found an average of 37 plant species in each plot; species richness was highest in the bog woodland vegetation type and lowest in the zonal forest vegetation type. We detected overdispersion in our model analysing the density of western redcedar trees; we, therefore, chose to reanalyse our model with a negative binomial distribution (Zuur et al., 2009). The density of western redcedar trees was significantly higher in vegetation plots with shorter MFI ($p < .01$) and model averaging delineated with 95% confidence intervals (based on AIC_c) indicated that the model containing only the variable MFI was the best predictor of western redcedar density (Table 2a). The abundance of traditional plants was significantly greater in plots with shorter MFI ($p < .01$), flatter terrain ($b = 0.021$, $z = 2.902$, $p < .01$), in close proximity to habitation sites ($b = -0.009$, $z = -1.993$, $p < .05$) and declined significantly at higher elevations ($b = -0.0139$, $z = -2.685$, $p < .01$; Table 2b; Figure 3). Model averaging delineated with 95% confidence intervals (based on AIC_c) indicated that the predictors aspect, elevation, distance to habitation, slope and MFI were of relatively equal importance and were included in the final model selection (Table 2b). Regression coefficients with 95% and 99% confidence intervals are plotted for the response variable percent cover of traditional food plants (Figure 4). Additional model selection criteria and validation are provided in Appendix S2 in the Supporting Information.

3.3 | Transect data: aboveground fire evidence

Fire-scarred trees and burned CMTs were more prevalent in transects near former habitation sites when compared with control sites (Welch two sample *t*-test: [$t = -4.1015$, $df = 27.699$, $p < .001$; Figure 3a fire-scarred trees], [$t = -3.6088$, $df = 26.64$, $p < .001$; Figure 3b CMTs]). The majority of trees with fire evidence were found 10–20 m (35%) and 20–30 m (46%) from the present-day forest edge. Dating of trees surrounding former habitation sites and control sites confirmed that most trees (80%) exceeded 200 years of age.

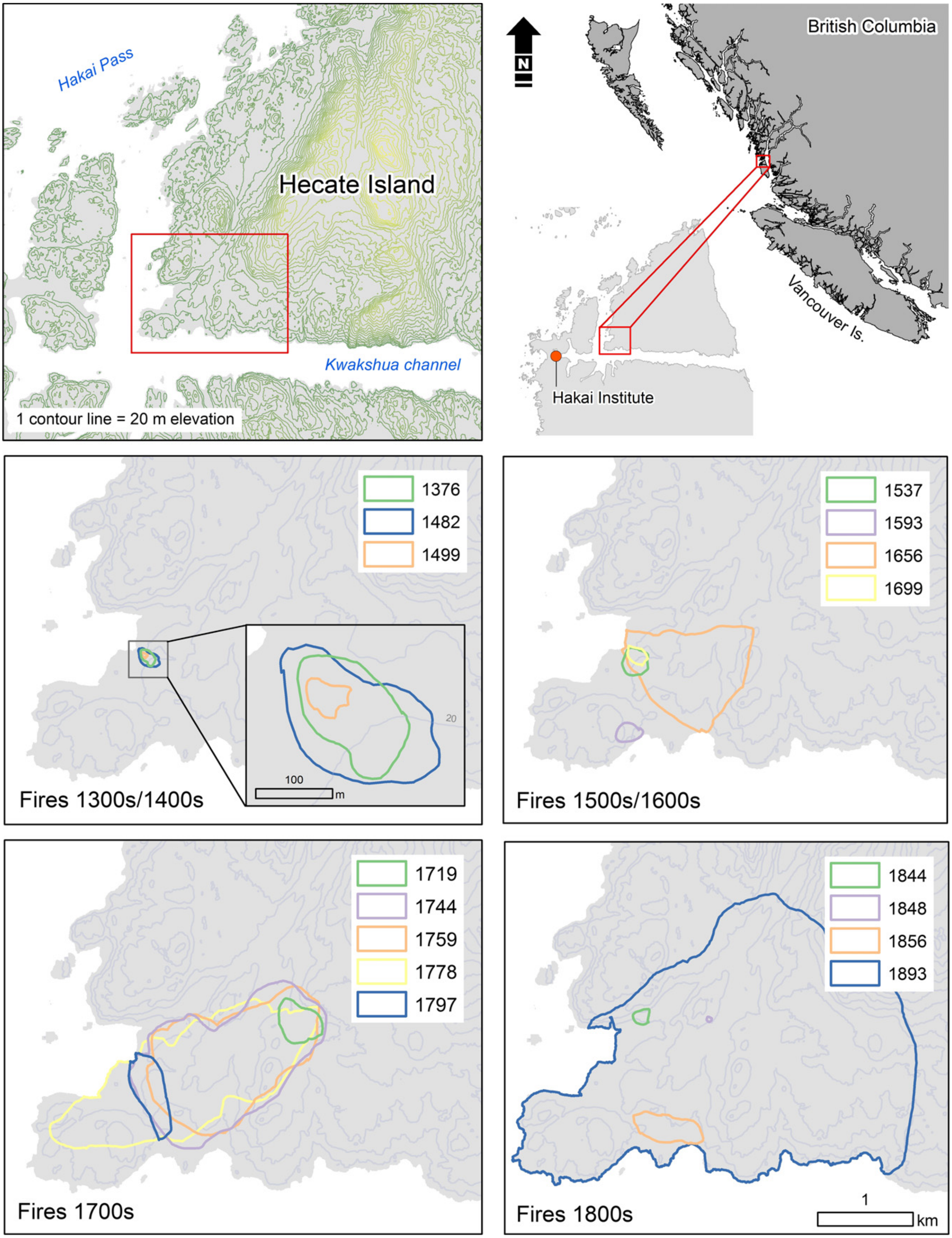

FIGURE 2 The spatial extent of 16 historic fire events derived from fire-scarred trees and post-fire stand establishment from 30 fire-history plots located on Hecate Island, British Columbia, Canada. The fire record extends from the first detected fire in 1376 to the last detected fire in 1893

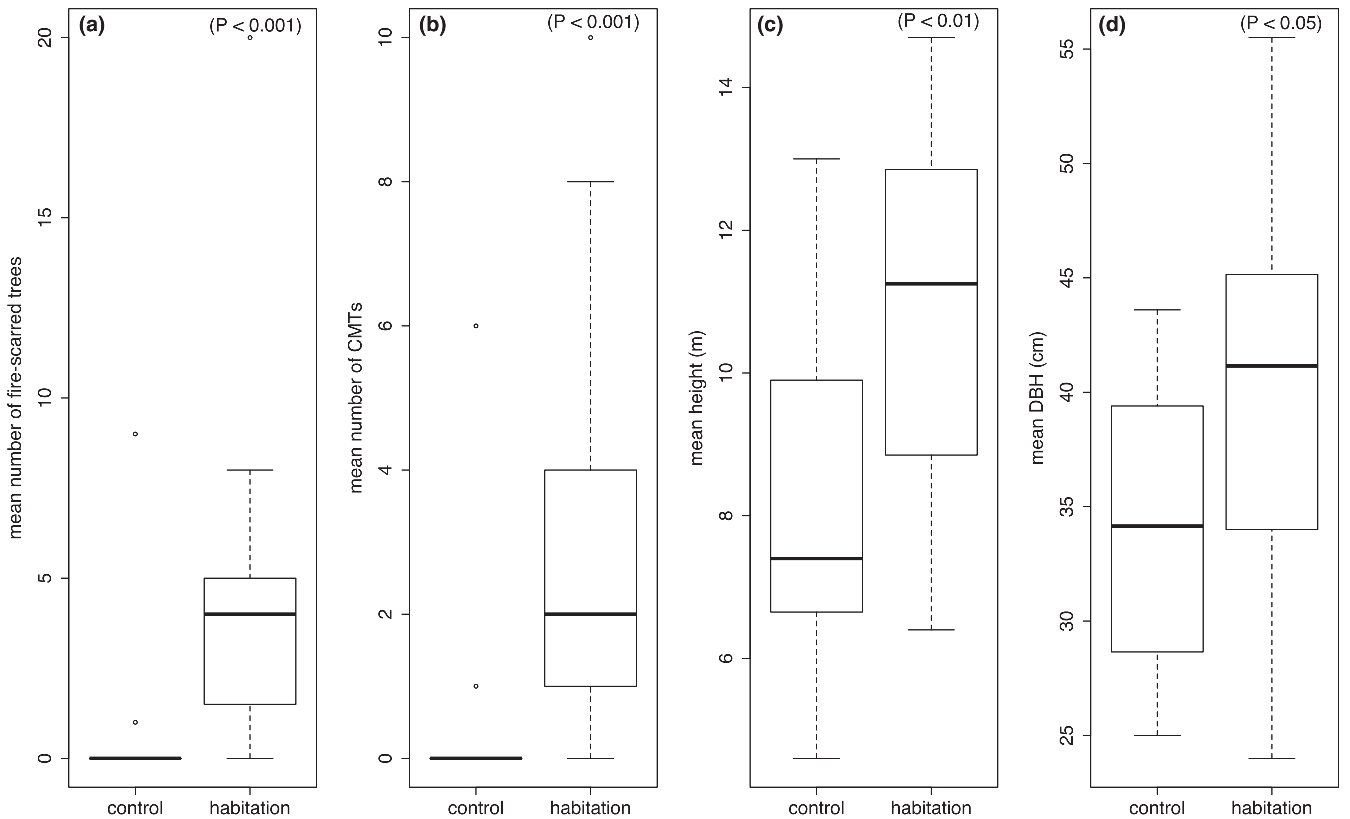

FIGURE 3 Box and whisker plots of the presence of fire evidence in forests surrounding former habitation and control sites (n = 20) located on 15 islands on the central coast of British Columbia, Canada (Figure 1). Boxes represent the second and third quartile ranges and the centreline is the median. Circles represent outliers. The abundance of fire-scarred trees (a, $p < .001$) and fire-scarred culturally modified trees (CMTs) (b, $p < .001$) were significantly greater in transects near former habitation sites. Trees were also significantly taller (c, $p < .001$) and had larger diameter at breast height (DBH) (d, $p < .05$) in former habitation sites compared to control sites

TABLE 2 Model selection using Akaike information criterion for small sample sizes (AIC_c) for 12 generalized linear mixed-effects models (GLMM) that describe (a) the density of western redcedar in vegetation plots; and (b) the abundance of traditional plants with six fixed predictor variables (elevation, slope, aspect, mean fire interval [MFI], distance to habitation site in metres and distance to shoreline in metres) and one random model effect (vegetation type [four types]). K = number of model parameters, ΔAIC_c = change in AIC score from the top model, w_i = AIC_c model weight, ER = top model weight divided by i model weight. Full results and model validation are provided in Appendix S2 in Supporting Information

Model	K	ΔAIC_c	w_i	ER	Parameters
(a) Density of western redcedar in vegetation plots					
1	1	0.00	0.26	1.00	MFI
2	2	1.84	0.10	2.60	MFI, distance to habitation
3	2	2.14	0.10	2.60	MFI, slope
4	2	2.30	0.08	3.25	MFI, aspect
5	2	2.65	0.07	3.71	MFI, elevation
6	3	3.02	0.06	4.33	MFI, distance to habitation, slope
7	5	3.71	0.05	5.20	MFI, distance to habitation, slope, aspect, vegetation type
(b) Abundance of traditional plants					
1	2	0.00	0.20	1.00	Distance to habitation, elevation
2	4	0.03	0.20	1.00	Distance to habitation, elevation, slope, MFI
3	4	0.49	0.16	1.25	Distance to habitation, elevation, slope, aspect
4	5	0.91	0.13	1.53	Distance to habitation, elevation, aspect, slope, MFI
5	3	1.80	0.08	2.50	Distance to habitation, elevation, MFI

Consistent with Trant et al. (2016), trees were also taller near former habitation sites (t = −3.8868, df = 37.587, p < .01; Figure 3c) and had larger DBH (t = −2.7542, df = 36.786, p < .05; Figure 3d). Most fire evidence was found on culturally modified western redcedar trees. There was no significant difference in the number of trees and the average number of pieces of CWD between transects in former habitation and control sites (Figure S1.1).

3.4 | Temporal and spatial patterns of lightning

There have been two lightning strikes on Hecate Island since 1999. Both strikes occurred in December and were accompanied by heavy precipitation (>30 mm in the 24-hr period; Figure 5). In total, 396 strikes occurred in the 2,000-km^2 study area from 1999–2014, and of these strikes, 108 hit land and 17 occurred in summer months (May 1st to September 30th; Figure 5). The odds of lightning striking the sea were higher than striking the land in both winter and summer months (p < .01; Figure 5). Cumulative precipitation in the 14-day period prior to 94% of lightning strikes in the summer months exceeded 20 mm, indicating that fuel moisture levels would likely not have lowered to a point (*c.* 30–40% moisture content) that fire could spread (Agee, 1993; Daniels & Gray, 2006; Whitlock et al., 2015).

4 | DISCUSSION

Multiple lines of evidence derived from fire scars, stand ages, plant community characteristics and lightning strike densities are in

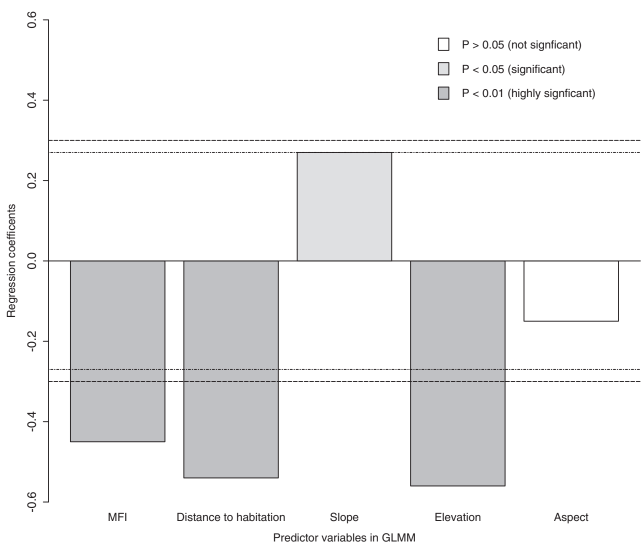

FIGURE 4 Regression coefficients demonstrate the relationship between the variables mean fire interval (MFI), distance to former habitation site, slope, elevation and aspect and the abundance (percent cover) of traditional plants found in the study area. Selected variables are the final predictors included in the generalized linear mixed-effects model (GLMM) (Table 2b). Lines and grey shading present 95% and 99% confidence intervals

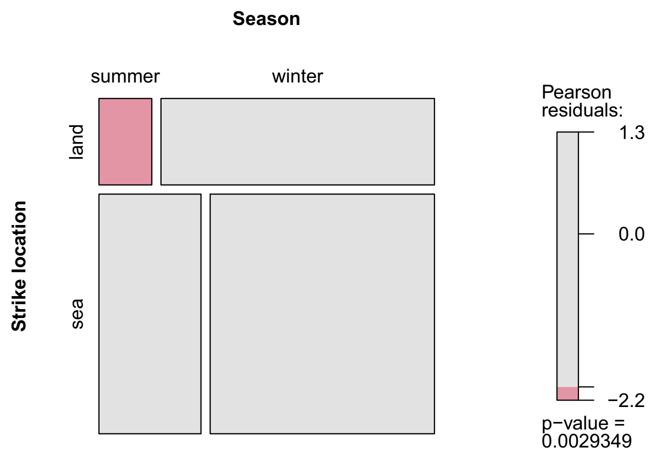

FIGURE 5 The probability of lightning striking the land in summer (shaded in pink) is significantly lower (p = .002) than lightning striking the sea in winter in the 2,000 km^2 study area on the central coast of British Columbia, Canada. The size of each rectangle is proportional to the observed frequencies of lightning recorded during 1999–2014. Rectangles are shaded to reflect the magnitude and significance of the Pearson residuals. Low Pearson residuals indicate a good model fit

opposition to the hypothesis that historic fires resulted from natural lightning ignitions. Our data suggest that lightning is too rare to explain the temporal and spatial patterns of historic fire activity in the study area (Figure 5). Our data also support our second hypothesis that fires (whether accidental or intentional) were associated with human occupation of the land, and we find that fires of human origin occurred regularly in our fire-history data, as reflected in their timing, location, severity and effects to vegetation. Our data show that our third hypothesis that humans intentionally used fire to manage resources is consistent with evidence collected in our study area, although further research on this is warranted. Although we strongly suspect that anthropogenic burning was intentional and widespread in the study area, evaluating this third hypothesis requires that additional fire-history reconstructions and ethnographic data be collected elsewhere in perhumid rain forests (Table 1).

4.1 | Temporal attributes of historic fire activity

Low- and mixed-severity fires occurred approximately every 39 years for almost six centuries prior to cultural changes in the region in the late 19th and early 20th centuries (Hoffman, Gavin, & Starzomski, 2016). Because the process of fire scarring is highly variable and dependent on geographical location and fire tolerance of tree species (Tepley & Veblen, 2015), we provide a minimum estimate of the number of historic fire events (16) and acknowledge that the distribution of fire intervals recorded at the plot level is skewed to fire intervals that are longer than those of the composite MFI expressed at the stand or landscape scale (Table S1.3). This is expected since not every fire event recorded in the study area was intense enough to scar the majority of trees, and differences in fuel moisture and fuel availability resulted in unburned areas within fire boundaries (Johnson & Gutsell, 1994).

The ecological effects of fire activity in coastal temperate rain forests are assumed to be localized with year-round wet conditions overriding human ignitions (Whitlock et al., 2015). In perhumid rain forests, climate is assumed to be the primary driver of the distribution and composition of vegetation and lightning-ignited fires are estimated to occur every few hundred or even few thousand years (Daniels & Gray, 2006; Lertzman et al., 2002). Despite these findings, previous research on human and climate drivers of fire activity in our study area indicates that humans may have utilized favourable climate conditions such as periodic extreme droughts to manage resources with fire (Hoffman, Gavin, & Starzomski, 2016; Macias Fauria & Johnson, 2006). Although we were unable to determine the exact timing of fire events, ethnographic accounts of intentional burning in nearby areas suggest that burning occurred in the late summer after berries had been harvested and the vegetation was drier (Turner, 1999, 2014).

Human-driven fire activity has also been documented in other island environments and temperate rain forests globally. For example, in New Zealand where lightning is rare, human ignitions explain much of the variation in historic fire activity and in regional patterns of vegetation (McWethy et al., 2013). Researchers have also demonstrated that indigenous people were an important ignition source in coastal temperate rain forests in Patagonia and Tasmania (Whitlock et al., 2015). Although lightning ignitions are also relatively rare in perhumid coastal temperate rain forests in British Columbia, to this point humans have not been considered drivers of historic fire activity.

4.2 | Spatial aspects of historic fire activity

Several studies in North America have been unable to distinguish human influences on historic fire activity because the majority of research has taken place in fire-prone ecosystems where it is difficult to differentiate between lightning and human ignitions (Bowman et al., 2011; Lepofsky et al., 2003; Walsh, Marlon, Goring, Brown, & Gavin, 2015). Although the impact and scale of historic anthropogenic burning in perhumid coastal temperate rain forests in British Columbia may seem geographically localized, a closer look at the study area reveals that although the majority of fires were relatively small (*c*. 3 ha) and low-severity, the location of fires near former habitation sites is a significant finding (Figure 3). There are *c*. 275 archaeological sites in the study area alone (McLaren et al., 2015) and thousands of sites in coastal temperate rain forests in British Columbia. The density of archaeological sites, together with compelling evidence of anthropogenic burning presented in this study, suggest that the scale of human-caused fires (whether intentional or not) in perhumid rain forests and their lasting ecological effects may be greater than previously believed.

4.3 | Patterns of lightning strikes

Lightning strike densities are strongly influenced by the proximity of cold-water bodies, elevation and diurnal heating and cooling cycles over land masses (Burrows & Kochtubajda, 2010). Unlike interior and mainland areas of Canada with seasonal patterns of lightning, lightning occurs year-round in offshore and Pacific coastal regions of British Columbia (Burrows & Kochtubajda, 2010). Inland areas of British Columbia have on average 15–33 days of lightning annually, compared to an average of 1–10 days of lightning in Pacific coastal regions (Burrows et al., 2002). Lightning strike densities in inland areas of British Columbia follow predictable temporal and spatial patterns, are positively correlated with elevation (most common at ~800 m a.s.l.) and occur in clusters where one fire ignition is estimated for every 50 lightning strikes (Burrows & Kochtubajda, 2010). This pattern is opposite to the spatial and temporal pattern of lightning observed in the study area, where lightning is most common in the winter months and strike densities are highest over the ocean (Figure 5). Although we acknowledge that the lightning dataset used in this study is short (15 years) and may not be representative of previous climatic periods, we find that characteristics of contemporary lightning strike densities do not correspond to or appear to explain the observed patterns of fire activity in the study area (Table 1).

4.4 | Ecological legacies of historic fire activity

Perhumid coastal temperate rain forests contain species that are poorly adapted to fire disturbances and lack traits to survive and colonize even after low- and moderate-severity fires (Banner et al., 2005). Western redcedar, western hemlock and Sitka spruce have low resistance to fire because of their relatively thin bark and shallow root systems (Agee, 1993). Despite these characteristics, we found that western redcedar trees were able to endure repeated low-severity fires and may be more fire tolerant than previously assessed. Western redcedar is a culturally important and highly valued species with many uses including canoe and house plank construction, as well as for firewood, clothing and medicine (Hebda & Mathewes, 1984; Turner, 2014). Frequent landscape burning directly behind habitation sites may have encouraged western redcedar regrowth and increased the density of culturally modified and fire-scarred western redcedar (Table 1) (Turner, 1999).

Indigenous people may have also intentionally increased the abundance of specific plants and affected the diversity of plant communities by regulating the size, frequency, intensity and timing of fires (Lepofsky & Lertzman, 2008; Turner, 1999, 2014). Although it is difficult to infer intentional fire-management systems from a forest that last burned more than 120 years ago, we found that the abundance of culturally important plants was correlated with fire activity (Figure 4; Table S1.4). These plants were clustered at low elevations near former habitation sites in open, flat and easily accessible areas. An increase in the presence of fire-scarred trees and burned CMTs 20–30 m from the present-day forest edge (areas with no below-ground evidence of shell midden) suggests that fires may not have started in the immediate vicinity of homes and were separate from habitation sites (Table 1). Oral histories have confirmed that habitation sites were often located very close (within a short walking distance ~5 min) to wetland burning sites on the Olympic Peninsula in Washington (Wray, 2009) and directly behind village sites in Haida Gwaii and on Vancouver Island (Turner, 1999). Potential fire-management techniques that may have been utilized close to habitation sites in the study area include using fire to fall large western red-cedar trees to make canoes and partially girdling and burning trees to create dry and easily accessible firewood in wet winter months (Turner, 1999, 2014). A counter-argument to the intentional use of fire in these sites may be the fact that fires were not more common on otherwise identical nearby control island sites, where the risk of intentional fire management to infrastructure was not present.

Although there are many documented plant-management techniques used by indigenous groups, burning was used in the Pacific Northwest of North America to maintain open habitats, which are typically richer in food resources compared to closed-canopy coniferous forests (Boyd, 1999; Storm & Shebitz, 2006; Wray, 2009). These open areas may have been easily accessible resource sites where berries were picked, trees were thinned and plants were gathered after burning (Table S1.2). Burning in different years and seasons may have created a diversity of forests in various stages of succession, thereby increasing the abundance and productivity of food plants in differing life stages (Lepofsky & Lertzman, 2008). There have been no documented fire ignitions or suppressions in the study area since the last detected fire in 1893. The abrupt end to fire activity in the late 19th century coincides with the relocation of indigenous groups to other islands or mainland areas of British Columbia (Table 1).

Anthropogenic burning left distinct temporal and spatial legacies in our study region. Our evidence is consistent with the hypothesis of intentional human fire ignitions, but also partially consistent with accidental ignitions (Table 1). We conclude that the history of fire on this landscape is largely anthropogenic, likely representing a mix of fires that were part of a system of intentional management and fires that were ignited unintentionally near habitations. Reconstructing fire histories in old growth coastal temperate rain forests is complex and combining multiple lines of evidence is required to test hypotheses about the origins of fires. We can pose the hypothesis, however, that centuries of anthropogenic burning (whether intentional or accidental) have left land-use legacies, which include a mosaic of vegetation types and successional stages, and an increase in the abundance of culturally important plants. A cessation of anthropogenic burning can explain why fire disappeared from our study area at the end of the 19th century, in contrast to its occurrence on average every 39 years over the previous six centuries.

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DATA ACCESSIBILITY

Supporting datasets can be accessed at DOI: 10.5061/dryad.r701q

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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