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Camille Giuliano and Terri Lacourse

2023

This article was originally published at:
https://doi.org/10.1002/ecs2.4416

Citation for this paper:

Giuliano, C., & Lacourse, T. (2023). Holocene fire regimes, fire-related plant functional types, and climate in south-coastal British Columbia forests. *Ecosphere*, *14*(2). https://doi.org/10.1002/ecs2.4416

Received: 2 September 2022 | Revised: 15 November 2022 | Accepted: 28 November 2022

DOI: 10.1002/ecs2.4416

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Holocene fire regimes, fire-related plant functional types, and climate in south-coastal British Columbia forests

Camille Giuliano | **Terri Lacourse**

Department of Biology and Centre for Forest Biology, University of Victoria, Victoria, British Columbia, Canada

Correspondence
Terri Lacourse
Email: tlacours@uvic.ca

Funding information
British Columbia Knowledge Development Fund, Grant/Award Number: 804365; Canada Foundation for Innovation, Grant/Award Number: 17214; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: 342003; Pacific Institute for Climate Solutions

Handling Editor: Carrie R. Levine

Abstract

Paleoecological records of past fire events and forest composition provide long-term ecological context for modern changes in fire regimes and forest dynamics. Here, we use pollen and contiguous macroscopic charcoal analyses of lake sediments from Pender Island, British Columbia, Canada to reconstruct changes in fire regimes over the last 10,000 years and investigate how these interact with changes in climate and forest composition with a focus on fire-related plant functional types. The relatively warm and dry early Holocene was characterized by high charcoal accumulation rates, fire episodes of moderate severity, and a mean fire return interval of 100 ± 27 years. Forests at the time were open-canopy *Pseudotsuga menziesii* forests with abundant fire endurer taxa (e.g., *Pteridium aquilinum*) that have a competitive advantage in regimes of frequent fire. Fire continued to occur every ~100 years, on average, during the establishment of *Quercus garryana* savanna communities; however, a decrease in charcoal peak magnitudes suggests the fire regime shifted to one characterized by smaller and/or lower intensity surface fires. As temperature and moisture deficits decreased in the mid- and late Holocene (i.e., after ~6000 calendar years before present), mean fire return intervals lengthened to 176 ± 54 years and increased variability in charcoal peak magnitudes suggests a mixed fire regime of low-moderate-intensity fires combined with infrequent crown or stand-replacing fires. Relatively stable and moderate climate, longer fire return intervals, and mixed-severity fires allowed *P. menziesii* (a fire resister) to dominate closed-canopy forests and for fire avoiders to gradually become more common forest constituents. Millennial-scale climate change has acted as the dominant driver of changes in both fire regimes and forest composition over the last 10,000 years; however, changes in fire-related plant functional types highlight the important role that interactions between vegetation and fire play in long-term fire regimes and forest dynamics.

KEYWORDS
charcoal accumulation, charcoal peak analysis, climate change, fire frequency, fire return interval, fire survival traits, lake sediments, macroscopic charcoal, pollen analysis, *Pseudotsuga menziesii*, *Pteridium aquilinum*, *Quercus garryana*

INTRODUCTION

Wildfires are one of the most common forms of natural disturbance in western North American forests, with regulatory effects on species traits, species interactions, community composition and structure, and ecosystem services including nutrient cycling and carbon storage (Hagmann et al., 2021; Harrison et al., 2021; McLauchlan et al., 2020). As temperatures and moisture deficits rise, wildfires are expected to steadily increase, with lengthened fire seasons and increases in yearly area burned, threatening human populations and infrastructure, and drastically increasing fire management costs (Abatzoglou & Williams, 2016; Flannigan et al., 2005; Hagmann et al., 2021; Halofsky et al., 2020). However, the degree to which wildfires will increase over time will vary widely depending on local climate, forest composition and structure, and land use (Halofsky et al., 2018). Understanding the long-term causes and consequences of wildfires and landscape management practices is becoming increasingly important from both ecological and societal perspectives. Wildfire regimes in many ecosystems have been unsustainably modified for centuries by human activities including various forms of fire management, fire suppression or exclusion, land clearing, and unintentional fires (Coogan et al., 2019; Harrison et al., 2021; Marlon, 2020; McLauchlan et al., 2020), limiting inferences about natural fire regimes that can be drawn from modern observations and historical data. Paleoecological studies of past fire regimes such as macroscopic charcoal analyses of lake sediments can be a powerful alternative as they provide the opportunity to examine relationships between fire dynamics and changes in forest composition and climate on long ecological timescales (Gavin et al., 2007). Fire scars in tree rings allow for annual-precision reconstructions of fire activity, but these records generally only extend a few centuries at most (McLauchlan et al., 2020; Remy et al., 2018). Analyses of macroscopic charcoal in lake sediments provide lower temporal resolution than tree rings but much longer records of landscape-scale wildfire activity, which are useful in assessing if and when contemporary wildfires exceed historical conditions (Conedera et al., 2009; Marlon, 2020; Remy et al., 2018; Whitlock & Larsen, 2001).

Using a synthesis of 679 sedimentary charcoal records and climate model simulations, Daniau et al. (2012) demonstrated that, at a global scale, changes in temperature and to a lesser extent moisture levels have been the dominant drivers of biomass burning over the past 21,000 years. The availability of fuel and sources of ignitions are additional important controls on biomass burning (Krawchuk et al., 2009). Sedimentary charcoal studies are common in western North America (Figure 1) and offer a general picture of the main shifts in the region's fire regimes over the Holocene. Previous work has shown that fire was uncommon throughout the region at the start of the Holocene, around 12,000 calendar years before present (cal yr BP), but increased over time as temperatures increased in the early Holocene (Walsh et al., 2015). By 10,000 cal yr BP, fire frequency was high at many sites in the Pacific Northwest (e.g., Brown et al., 2022, 2019; Prichard et al., 2009; Walsh et al., 2015, 2010, 2008; White et al., 2015). Warmer and drier climate in the early Holocene coupled with increased seasonality would have facilitated this period of more frequent fire. Fire activity decreased after 8000 cal yr BP throughout much of the region, reaching an overall low in biomass burning ~5500 cal yr BP (Walsh et al., 2015). At a number of sites, biomass burning increased in the late Holocene despite decreased temperatures and increased precipitation, peaking around 900 cal yr BP (Walsh et al., 2015). This increase is often attributed to greater interannual climate variability and/or Indigenous burning practices (e.g., Brown & Hebda, 2002a; Brown et al., 2019; Hoffman et al., 2016; Walsh et al., 2015). Over the course of the Holocene, millennial-scale changes in climate and fire regimes were accompanied by changes in forest composition and structure (e.g., Gavin et al., 2013, 2007; Long et al., 2007; Marlon et al., 2006; Walsh et al., 2008). In addition, strong feedbacks exist between fire regimes and plant communities such that vegetation properties and plant traits have the potential to both shape and be shaped by fire regimes (Brussel et al., 2018; Harrison et al., 2021; Wirth, 2005).

Although there are a number of macroscopic charcoal studies in the Pacific Northwest (Figure 1), there are few studies in the fire-adapted *Pseudotsuga menziesii*-dominated forests of coastal British Columbia (BC). Furthermore, most charcoal records in or near coastal BC do not span the full Holocene (Derr, 2014; Gavin et al., 2003a; Lucas & Lacourse, 2013; Murphy et al., 2019; Sugimura et al., 2008) or do not use contiguous charcoal sampling methods (e.g., Brown & Hebda, 2002a, 2002b, 2003), which precludes quantification of fire return intervals. Here, we present a contiguous charcoal record for *P. menziesii*-dominated forests in south-coastal BC that spans the full Holocene. We use high-resolution macroscopic charcoal analyses on lake sediments from Pender Island, BC to quantify charcoal accumulation rates, fire frequency, and fire return intervals. We compare the inferred wildfire history to changes in forest composition from pollen analyses on the same sediments (Lucas & Lacourse, 2013), with emphasis on how changes in wildfire regimes interact with changes in the abundance of fire-related plant functional types. We then assess how changes in wildfire and vegetation history interact with climate over the last 10,000 years through comparison with independent proxies of paleoclimate.

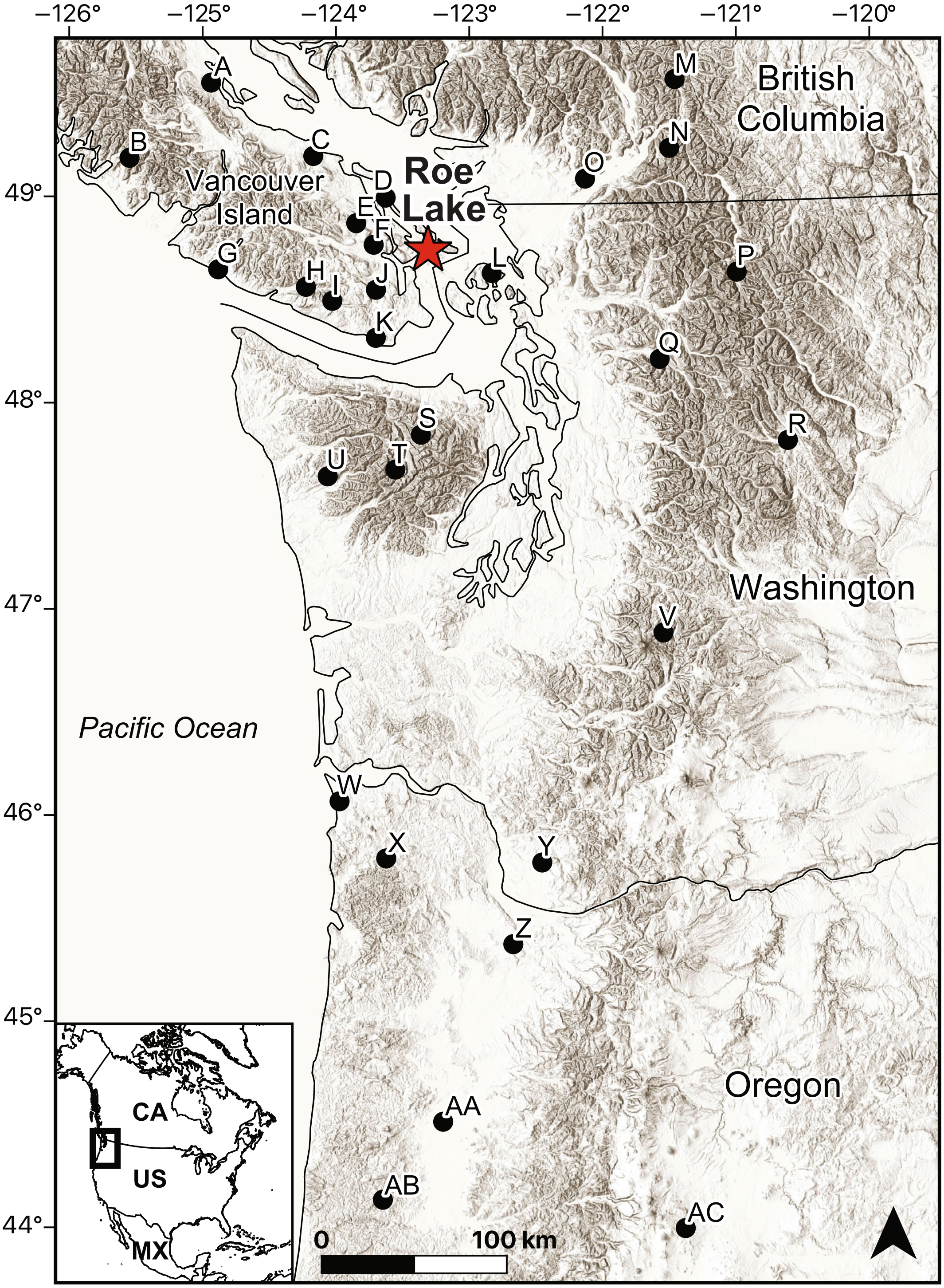

FIGURE 1 Map of the Pacific Northwest showing Roe Lake (star) on Pender Island, British Columbia, Canada and other macroscopic charcoal studies (circles) in the region: (A) Langley Lake (Brown et al., 2022), (B) Clayoquot Lake/Valley (Gavin et al., 2003a, 2003b), (C) Enos and Boomerang lakes (Brown & Hebda, 2002a), (D) Shingle Point (Derr, 2014), (E) Porphyry Lake (Brown & Hebda, 2003), (F) Somenos Lake (Murphy et al., 2019), (G) Whyac Lake (Brown & Hebda, 2002b), (H) Pixie Lake (Brown & Hebda, 2002b), (I) Walker Lake (Brown & Hebda, 2003), (J) Begbie Lake (Brown et al., 2019), (K) East Sooke Fen (Brown & Hebda, 2002b), (L) Moran State Park (Sugimura et al., 2008), (M) Frozen Lake (Hallett et al., 2003), (N) Mount Barr Cirque Lake (Hallett et al., 2003), (O) Chadsey Lake (Murphy et al., 2019), (P) Panther Potholes (Prichard et al., 2009), (Q) Kirk Lake (Cwynar, 1987), (R) Fish Lake (Walsh et al., 2018), (S) Moose Lake (Gavin et al., 2001), (T) Martins Lake (Gavin et al., 2001), (U) Yahoo Lake (Gavin et al., 2013), (V) Sunrise and Shadow lakes (Walsh et al., 2017), (W) Taylor Lake (Long et al., 2007), (X) Lost Lake (Long et al., 2007), (Y) Battle Ground Lake (Walsh et al., 2008), (Z) Lake Oswego (Walsh et al., 2018), (AA) Beaver Lake (Walsh et al., 2010), (AB) Little Lake (Long et al., 2007), and (AC) Tumalo Lake (Long et al., 2011).

MATERIALS AND METHODS

Roe Lake (48°46′59″ N, 123°18′11″ W, 100 m above sea level) is located on Pender Island in southwestern BC, Canada (Figure 1) within the Gulf Islands National Park Reserve. Climate in the region is under the dominating influence of the Pacific high-pressure system in summer and the Aleutian low-pressure system in winter. Summers are warm and dry, and winters are mild and rainy. On Pender Island, mean annual precipitation is about 835 mm, with summers receiving only about 160 mm, and mean winter and summer temperatures are 4.8 and 16.7°C, respectively (Wang et al., 2016). Climatic conditions are heavily influenced by the Vancouver Island Ranges to the northwest and the Olympic Mountains (USA) to the south, which result in a rain shadow and drier climate relative to surrounding areas. Forests in this rain shadow, on eastern Vancouver Island and adjacent islands, are dominated by *P. menziesii* with scattered patches of *Quercus garryana* parkland or savanna (Meidinger & Pojar, 1991). Similar forest and savanna communities also occur in lowlands to the south, in the Puget Trough in Washington and the Willamette Valley in Oregon (Franklin & Dyrness, 1973). Many of these communities are under pressure from human activity, urban development, and invasive species.

Roe Lake has a surface area of 3 ha, a maximum water depth of 9.5 m with no current inflowing streams, and a catchment of about 100 ha. Forests around the lake consist mostly of *P. menziesii* but *Thuja plicata*, *Abies grandis*, and *Acer macrophyllum* are also common. Understorey vegetation is dominated by *Gaultheria shallon* and *Symphoricarpos albus* shrubs, and *Polystichum munitum* and *Pteridium aquilinum* ferns. *Alnus rubra* occurs along the lake margin. *Quercus garryana* and *Arbutus menziesii* are present on nearby ridges, especially on the east side of the lake.

In May 2011, a 903-cm-long sediment core was collected near the center of Roe Lake in 9.14 m of water, using a 6.25-cm diameter gravity corer for the sediment–water interface and uppermost sediments, and a 5-cm diameter Livingstone piston corer for sediments below 45 cm. The chronology for the Roe Lake sediment core is based on four AMS ^{14}C ages on plant macrofossils (Table 1), the age of the Mount Mazama tephra (Egan et al., 2015), and 19 ^{210}Pb measurements on the uppermost 41 cm (Appendix S1: Table S1 and Figure S1). AMS ^{14}C ages were calibrated to calendar years using the IntCal20 data set (Reimer et al., 2020). The age-depth model (Figure 2) was built using Bayesian approaches in *bacon* 2.5.4 (Blaauw & Christen, 2011) and *plum* 0.1.5 (Aquino-López et al., 2018) in R (R Core Team, 2022). The mean of this model is not significantly different from a simple linear interpolation model, as is the case with many *bacon* models (Lacourse & Gajewski, 2020). The age-depth model for the uppermost sediments built in *plum* is very similar to an age model based on a constant rate of supply (Appleby, 2001); age estimates from the two modeling approaches typically differ by only a few years. However, the Bayesian approaches in *bacon* and *plum* provide more conservative estimates of error as well as the ability to anchor the two models via the uppermost ^{14}C age.

The lake sediment core was sampled contiguously for charcoal analysis by collecting 1 cm^3 (or occasionally 2 cm^3) of sediment along the full length of the core. The uppermost sediments (0–45 cm) were sampled every 0.5 cm and the rest of the sequence was sampled at 1-cm intervals. Each sediment sample was treated with 3% H_2O_2 for 24 h and then gently rinsed through a 150-μm sieve with distilled water. Charcoal particles, identified as black, opaque, angular, and relatively shiny (Whitlock & Larsen, 2001), were enumerated and each particle was assigned to one of three size classes (150–250 μm, 250–500 μm, and >500 μm) based on its longest axis. *CharAnalysis* 1.0 (Higuera et al., 2009) was used for statistical analysis of the charcoal concentration data. These data were interpolated to the median sample resolution of 13 years and charcoal accumulation rates (CHAR) were calculated using total charcoal concentrations and modeled sedimentation rates. Background CHAR was estimated using a 900-year locally weighted

TABLE 1 AMS ^{14}C and calibrated ages for the lake sediment core from Roe Lake, British Columbia, Canada.

Depth (cm)	Material	$\delta^{13}C$ (‰)	Radiocarbon age (^{14}C yr BP ±1σ)	2σ calendar age range (cal yr BP)	Lab code[a] or source
117.5	Male *Thuja plicata* cone	−25.3	1323 ± 15	1178–1293	NZA-37783
385	Wood	−25.0	4411 ± 20	4876–5045	NZA-37784
573.0–573.5	Mount Mazama tephra	…	…	7584–7682	Egan et al. (2015)
614.5	Wood	−27.9	7125 ± 25	7875–8005	NZA-37785
892.25–894.0	Organic lake sediment	−26.9	8780 ± 50	9555–10,115	Beta-313896

Abbreviation: cal yr BP, calendar years before present.

[a] NZA: Rafter GNS Science, Lower Hutt, New Zealand; BETA: Beta Analytic Inc., Miami, Florida.

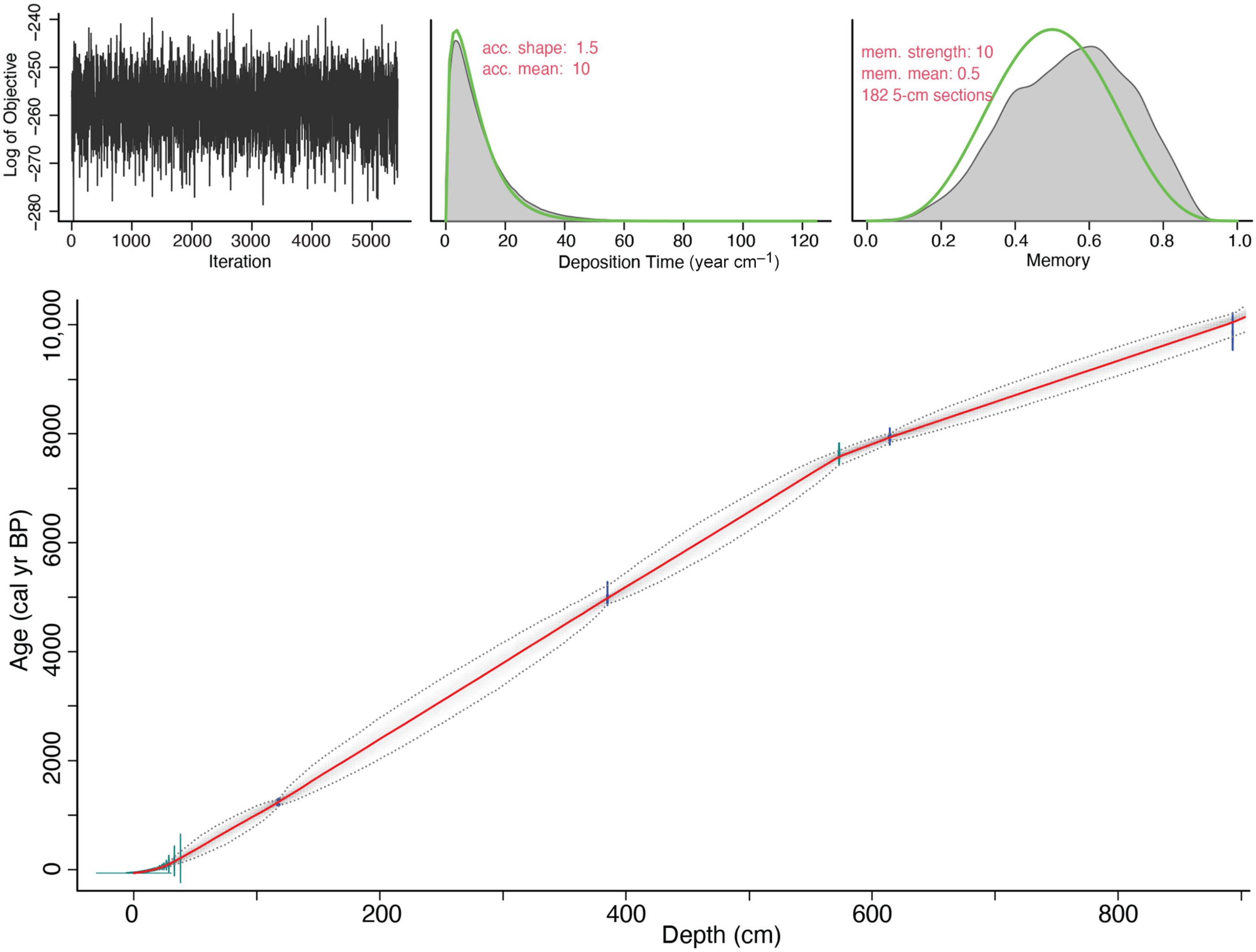

FIGURE 2 Age-depth model for Roe Lake, British Columbia, Canada based on ^{14}C ages (Table 1) and ^{210}Pb ages (Appendix S1: Table S1) and built using default settings in *bacon* 2.5.4 (Blaauw & Christen, 2011) and *plum* 0.1.5 (Aquino-López et al., 2018). Gray bands are 95% credible intervals. Top panels show Markov Chain Monte Carlo iterations (left) and prior (green) and posterior (gray) distributions for deposition times (acc.; middle) and memory (mem.; right). cal yr BP, calendar years before present.

regression robust to outliers and subtracted from the interpolated CHAR series to identify peaks in CHAR. The 99th percentile of a Gaussian mixture model was used to determine a local threshold to differentiate charcoal peaks associated with fire episodes (i.e., one or more fire within the 13-year sample resolution) from noise-related variation in CHAR (Gavin et al., 2006). These peaks were then used to calculate fire return intervals (FRIs) and mean FRIs over 1000-year intervals. Charcoal peak magnitude was used to assess fire severity and/or proximity (Higuera et al., 2014, 2009). The resulting fire history provides a minimum record of fire activity with FRIs representing years between landscape-level fire episodes, rather than time between individual fires at a single point in space. Change-point analysis was used to identify significant temporal changes in CHAR (Killick & Eckley, 2014).

Pollen data for Roe Lake were originally published in Lucas and Lacourse (2013), which describes the site's Holocene vegetation history in detail. These data were combined with additional pollen analyses to increase the temporal resolution of the pollen record. All samples were prepared in the lab following the same procedure. Sediment samples (1 cm^3) were treated with 10% KOH (8 min), concentrated HF, and acetolysis solution (3 min), and mounted in silicone oil. One tablet of *Lycopodium* spores (batch number 177745, 18,584 ± 829 spores) was added to each sample prior to chemical processing to calculate pollen accumulation rates (PAR). Between 500 and 600 terrestrial pollen and spores were identified in each sample. *Alnus* pollen were differentiated according to May and Lacourse (2012). Pollen and spore percentages are based on the sum of all terrestrial pollen and spores. For numerical zonation of the pollen record, constrained cluster analysis based on information content (Bennett, 1996) was conducted on all terrestrial taxa exceeding 2% of the sum in at least one sample. Palynological richness was calculated using a rarefaction sum of 500 (Birks & Line, 1992).

Pollen and spore taxa were classified into one of five fire-related plant functional types, according to Rowe (1983), Agee (1993), Wirth (2005), and USDA (2021): resister, endurer, evader, invader, or avoider (Appendix S1: Table S2). Resisters are typically shade-intolerant taxa with thick bark that allows the aboveground portion of the plant to survive low- to moderate-severity fire (e.g., *P. menziesii*). Endurers survive below ground and can quickly resprout from roots or rhizomes, giving them a competitive advantage in regimes with frequent, severe fires (e.g., *P. aquilinum*). Evaders are typically killed by fire but have seed banks in the soil or canopy that allow for rapid postfire germination (e.g., *Shepherdia canadensis*). Invaders are also usually killed by fire but can quickly recolonize burned sites due to prolific wind-dispersed seeds (e.g., *A. rubra*, *Pinus contorta*). Populations of *P. contorta* in coastal BC (i.e., var. *contorta*) typically lack serotinous cones that would classify it as a fire evader. Avoiders are easily killed by fire and only slowly return to disturbed sites (e.g., *Tsuga heterophylla*). When fires do occur, avoider taxa are typically associated with infrequent, stand-replacing crown fires. Classification of pollen and spore taxa was based on fire adaptation of mature plants rather than juveniles, which as a general rule tend to be fire avoiders. Taxa were not assigned to a fire survival category if there was little to no information on adaptation to fire or if they correspond with large taxonomic groups or morphotypes, rather than individual taxa. On average, only 3% of all pollen and spores in each sample was not categorized, with up to 10% uncategorized in assemblages with abundant Cyperaceae and Rosaceae, both of which were too broad to assign to a single category.

RESULTS

Lake sediment chronology and stratigraphy

The age-depth model for the Roe Lake core (Figure 2) estimated a basal age of 10,138 cal yr BP (10,160–10,340 cal yr BP). Modeled sedimentation rates for the core are typically between 0.07 and 0.13 cm year^{-1}, except in the uppermost 20 cm where rates reach a maximum of 0.5 cm year^{-1}. The 903-cm core is composed of uniform dark brown organic lake sediment (gyttja) with a tephra layer at 573 cm. Major element concentrations determined by electron microprobe analysis (Lucas & Lacourse, 2013) indicate that the tephra derives from the mid-Holocene eruption of Mount Mazama (Egan et al., 2015).

Charcoal accumulation and fire history

Mean charcoal concentration in the Roe Lake sediment record is 39.5 pieces cm^{-3}; however, charcoal concentrations are generally higher before 7000 cal yr BP, reaching a maximum of 182 pieces cm^{-3} around 8260 cal yr BP (Figure 3). Charcoal concentrations for the three size classes follow similar trends in similar proportions throughout the entire record. Mean CHAR for the entire record is 3.6 pieces cm^{-2} year^{-1} with a maximum of 18.1 pieces cm^{-2} year^{-1} (Figure 3). The median signal-to-noise index (Kelly et al., 2011) is 3.3, which supports peak analysis of the Roe Lake charcoal record. A total of 71 charcoal peaks were identified as statistically significant over the last 10,000 years (Figure 4), resulting in a mean FRI of 142 ± 28 years (mean and 95% bootstrapped confidence interval). However, years between individual fire episodes vary considerably from a minimum of 26 years to a maximum of 689 years. All of the significant peaks in CHAR, except one, consist mostly or exclusively (55%–100%) of charcoal pieces >250 μm (Figure 3), providing good evidence that the identified fire episodes represent local wildfires, that is, within the surrounding ~5 km (Adolf et al., 2018). The peak in CHAR at 5540 cal yr BP is mostly (63%) composed of charcoal in the smallest size class (150–250 μm). Change-point analysis on CHAR identified two statistically significant charcoal zones delimited at 7190 cal yr BP, which we use below to summarize the charcoal record.

Charcoal Zone 1 (10,140–7190 cal yr BP) is characterized by high CHAR and frequent charcoal peaks of moderate magnitude (Figures 3 and 4). Within this 2950-year period, mean CHAR is 6.7 pieces cm^{-2} year^{-1} and 28 charcoal peaks were identified, resulting in a mean FRI of 100 ± 27 years. Fire frequency is between 10 and 11 peaks 1000 year^{-1} until 8080 cal yr BP and then gradually decreases to 6 peaks 1000 year^{-1} by the end of the zone. Charcoal peak magnitude is moderate with a mean peak magnitude of 38 pieces cm^{-2} peak^{-1}. The highest charcoal peaks in this zone (at 8260 and 7690 cal yr BP) reached magnitudes of 101 and 120 pieces cm^{-2} peak^{-1}, respectively.

Charcoal Zone 2 (7190 cal yr BP to present) is characterized by lower CHAR and less frequent fire (Figures 3 and 4). CHAR never exceeds 10 pieces cm^{-2} year^{-1} during this interval. Mean CHAR is 2.3 pieces cm^{-2} year^{-1} and 43 fires were identified, resulting in a mean FRI of 167 ± 44 years, although return intervals vary considerably with a minimum of 75 years at ~5330 cal yr BP and a maximum of 351 years at ~2540 cal yr BP. Fire frequency fluctuates much more in this longer zone than in Charcoal Zone 1, reaching 11 peaks 1000 year^{-1} around 5300 cal yr BP and decreasing to ~2 peaks 1000 year^{-1}

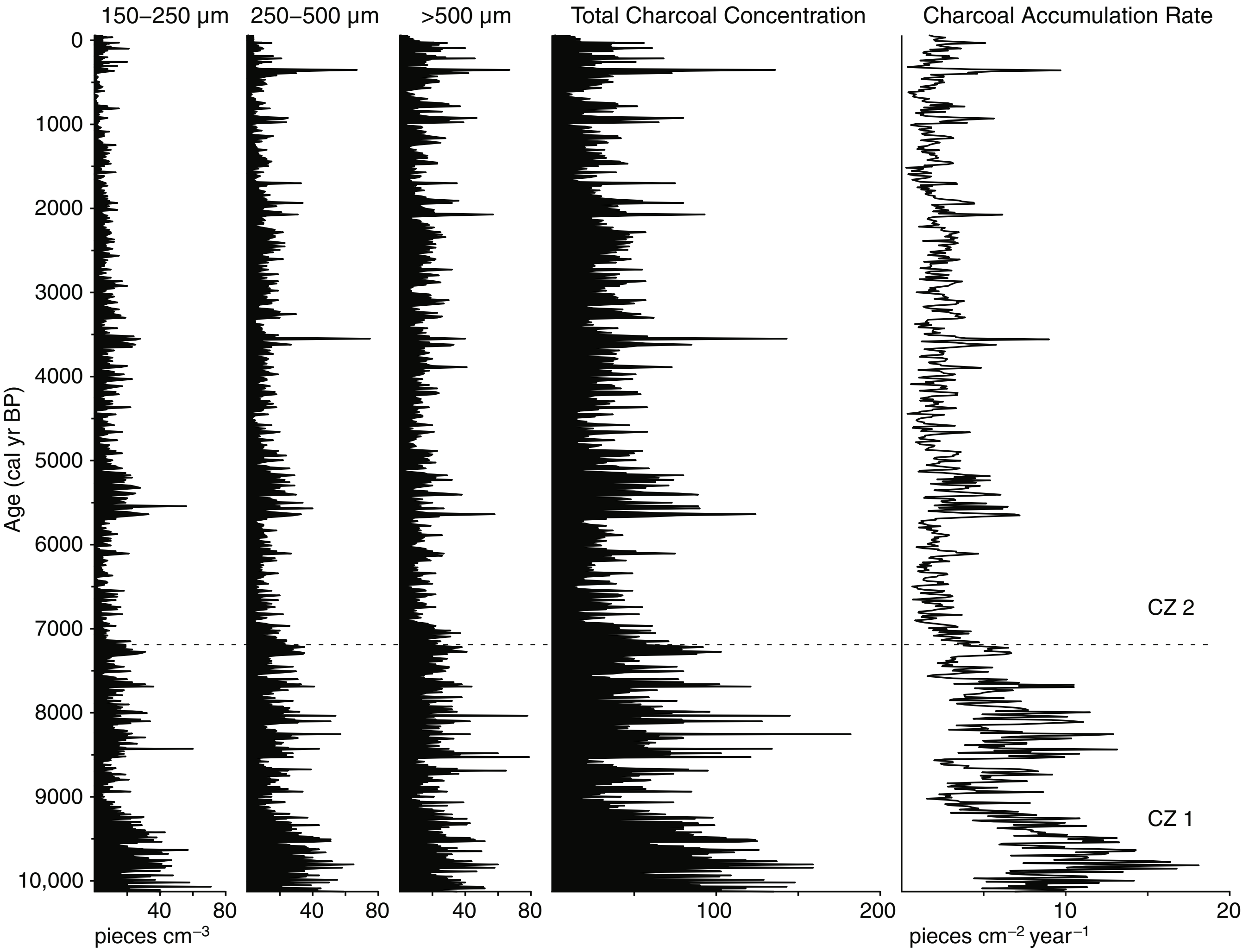

FIGURE 3 Macroscopic charcoal concentrations and total charcoal accumulation rates at Roe Lake. Concentrations are shown by size class and total concentration. Note changes in scale on the *x*-axes. Dashed horizontal line marks the change point in charcoal accumulation rates that delimit charcoal zones (CZ). cal yr BP, calendar years before present.

around 2800 cal yr BP. Mean peak magnitude is 24 pieces cm^{-2} peak^{-1}; however, variation in peak magnitudes is right-skewed with many small peaks (i.e., <20 pieces cm^{-2} peak^{-1}) interspersed among infrequent peaks that exceed 60 pieces cm^{-2} peak^{-1} (Figure 4). The highest magnitude charcoal peak for the entire record (204 pieces cm^{-2} peak^{-1}) occurred at ~390 cal yr BP. No fires had occurred in the preceding 365 years. Another large charcoal peak with a magnitude of 136 pieces cm^{-2} peak^{-1} occurred at ~5660 cal yr BP, after 455 fire-free years.

Pollen assemblages and forest composition

The median temporal resolution of the pollen record is 83 cal yr between samples. Cluster analysis identified two major pollen assemblage zones (Figure 5) with the boundary between them at 7510 cal yr BP, that is, only ~300 years before the change point in CHAR. In Pollen Zone 1, *A. rubra*, *P. contorta*, and Cupressaceae pollen account for 30%, 10%, and 6%, respectively, on average. *Pseudotsuga menziesii* increases from 4% at 10,100 cal yr BP to 26% by 7600 cal yr BP. Tree PARs, which provide a proxy for aboveground biomass (Knight et al., 2021), are ~3600 pollen cm^{-2} year^{-1}, on average, with most deriving from *A. rubra* type, *P. menziesii*, and *P. contorta*. *Alnus* spp. are prolific producers of well-dispersed pollen and their abundance in pollen records from western North America are often overrepresented relative to their abundance on the landscape (Minckley et al., 2008). The opposite is true for *P. menziesii*, which can account for as little as ~10% of the pollen sum at sites where it dominates the forest (Allen et al., 1999). Total herbs are relatively frequent at ~10% and include a diverse array of taxa including Poaceae, Cyperaceae, *Cicuta* type, *Angelica* type, *Plectritis*,

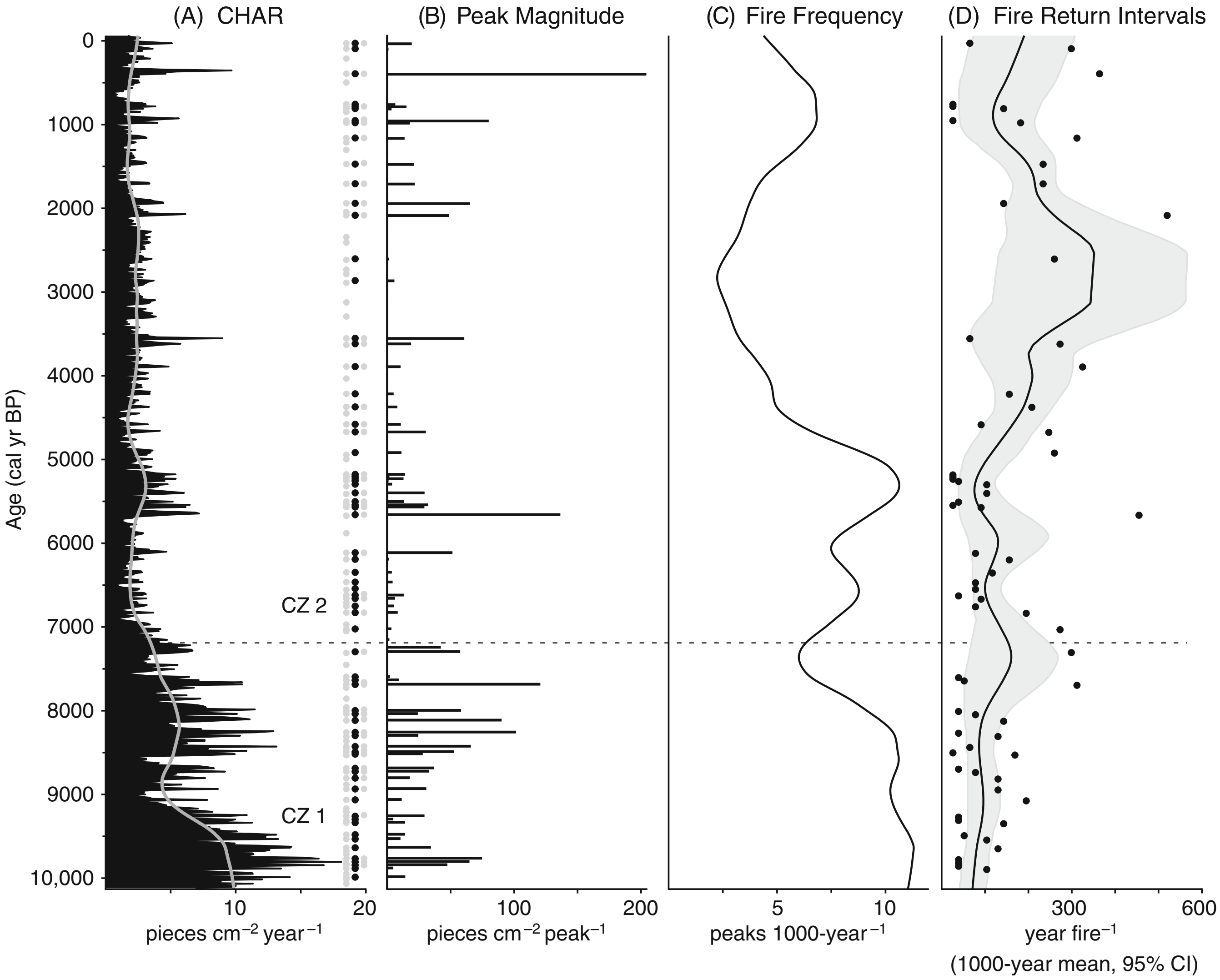

FIGURE 4 (A) Charcoal accumulation rates (CHAR) at Roe Lake with background rate (gray line) and charcoal peaks deemed significant at the 99th percentile (black circles). Gray circles show significant charcoal peaks at the 95th and 99.9th percentiles. (B) Charcoal peak magnitude. (C) Fire frequency smoothed in a 1000-year moving window. (D) Individual fire return intervals (black circles) and mean intervals with 95% bootstrapped confidence interval (CI) in gray. Dashed horizontal line marks the change point in CHARs that delimit charcoal zones (CZ). cal yr BP, calendar years before present.

and various Asteraceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, and Liliaceae. *Pteridium aquilinum* spores are abundant (~5%–20%), as are *Polypodium* spores (~5% before 9000 cal yr BP). The ratio of arboreal to nonarboreal pollen (AP/NAP) is <30 in Pollen Zone 1. Palynological richness is relatively high with a mean of 27 pollen and spore taxa, in large part because of the diversity of herbs and ferns, especially before 9000 cal yr BP.

Pollen Zone 2 is dominated by *A. rubra* and *P. menziesii*, both of which typically account for 25%–45% of the total pollen sum. Cupressaceae (5%–15%) and *T. heterophylla* (5%–10%) are important secondary components. *Quercus garryana* pollen begins to increase ~8000 cal yr BP, reaching a maximum of 16% at ~6500 cal yr BP, before decreasing to trace levels (≤2%) after 5000 cal yr BP. *Quercus garryana* typically accounts for 10%–30% of modern pollen assemblages in surface samples from *Q. garryana* stands (Allen et al., 1999). *Acer macrophyllum* increases to 2% during the peak in *Q. garryana*. Tree PARs are, on average, almost twice (i.e., 6200 pollen cm^{-2} year^{-1}) those of Pollen Zone 1 (Figure 6), with most pollen deriving from *P. menziesii* and *A. rubra* type. Herb pollen and fern spores account for only 2%, on average. AP/NAP exceeds 50 in much of Pollen Zone 2. Mean palynological richness is relatively low (19 pollen and spore taxa) with arboreal pollen accounting for 95% of the assemblages, on average. In general, Pollen Zone 2 consists of higher relative abundance of *P. menziesii* pollen, higher tree PAR, and low herb pollen and fern spore abundance compared with

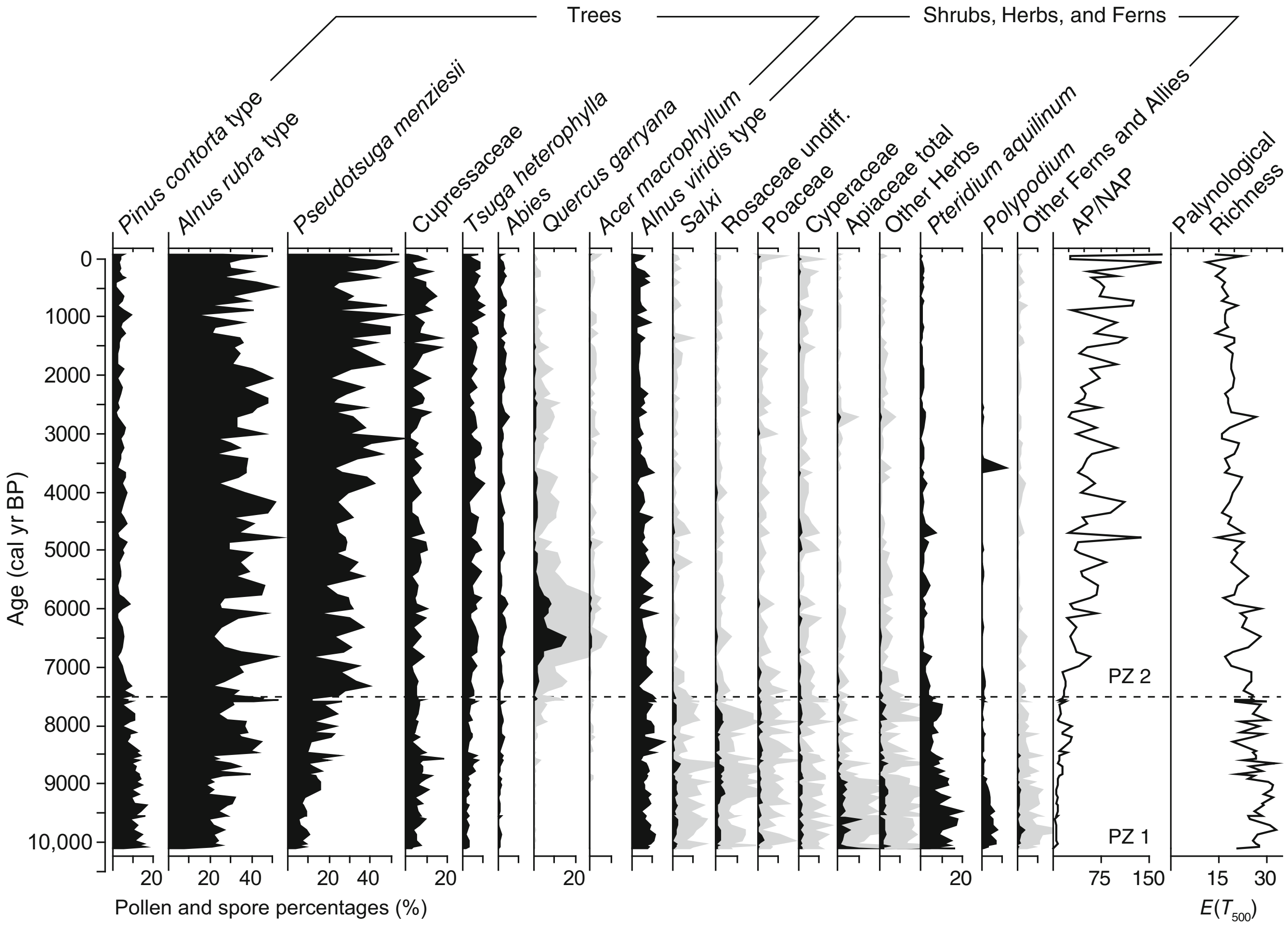

FIGURE 5 Pollen and spore percentages of major taxa for Roe Lake, British Columbia, Canada. Gray silhouettes for select taxa are 5× exaggeration of the data. Total Apiaceae is mostly *Cicuta*-type pollen. Dashed horizontal line delimits pollen assemblage zones (PZs) based on cluster analysis. AP/NAP, arboreal to nonarboreal pollen ratio. Palynological richness was calculated using a rarefaction sum of 500 pollen and spores per sample ($E(T_{500})$). cal yr BP, calendar years before present; undiff., undifferentiated.

Pollen Zone 1, reflecting a relatively more closed forest canopy after ~7500 cal yr BP.

Of the five different fire-related plant functional types, endurer and resister taxa varied the most over time (Figure 6). In Pollen Zone 1 (>7500 cal yr BP), endurers and resisters account, on average, for 17% and 13%, respectively, of the pollen record. After 7500 cal yr BP, resisters increase to a mean of 32%, while endurers decrease, on average, to only 5%. The trend among endurers is mainly controlled by *P. aquilinum*, *Polypodium*, and *Cicuta* type, whereas *P. menziesii* is the only true fire resister in the Roe Lake pollen record. Invaders and avoiders vary less over the course of the record with invaders decreasing from a mean of 52% to 46%, and avoiders representing 12% of the early record and 15% after 7500 cal yr BP. Common invaders include *P. contorta*, *Alnus viridis*, and *A. rubra*, and common avoiders include *T. heterophylla* and Cupressaceae. Fire evaders make up <1% of the pollen assemblages throughout the record.

DISCUSSION

Fire regimes, forest composition, and plant functional types

The paleoecological record from Roe Lake spans the last 10,000 years, revealing forests with *P. menziesii* (a fire resister) as the dominant conifer and a mean FRI of 142 ± 28 years. *Alnus rubra* (a fire invader) is abundant throughout the Roe Lake pollen record. Although some portion of this is likely associated with long-distance transport from regional sources (Allen et al., 1999; Minckley et al., 2008), this nitrogen-fixing tree would have been present on Pender Island in open, disturbed, and riparian areas, as it is today.

The early Holocene portion of the Roe Lake record (i.e., before 7200 cal yr BP) is marked by high charcoal accumulation, charcoal peaks of intermediate magnitude, and a mean FRI of 100 ± 27 years (Figure 4), suggesting

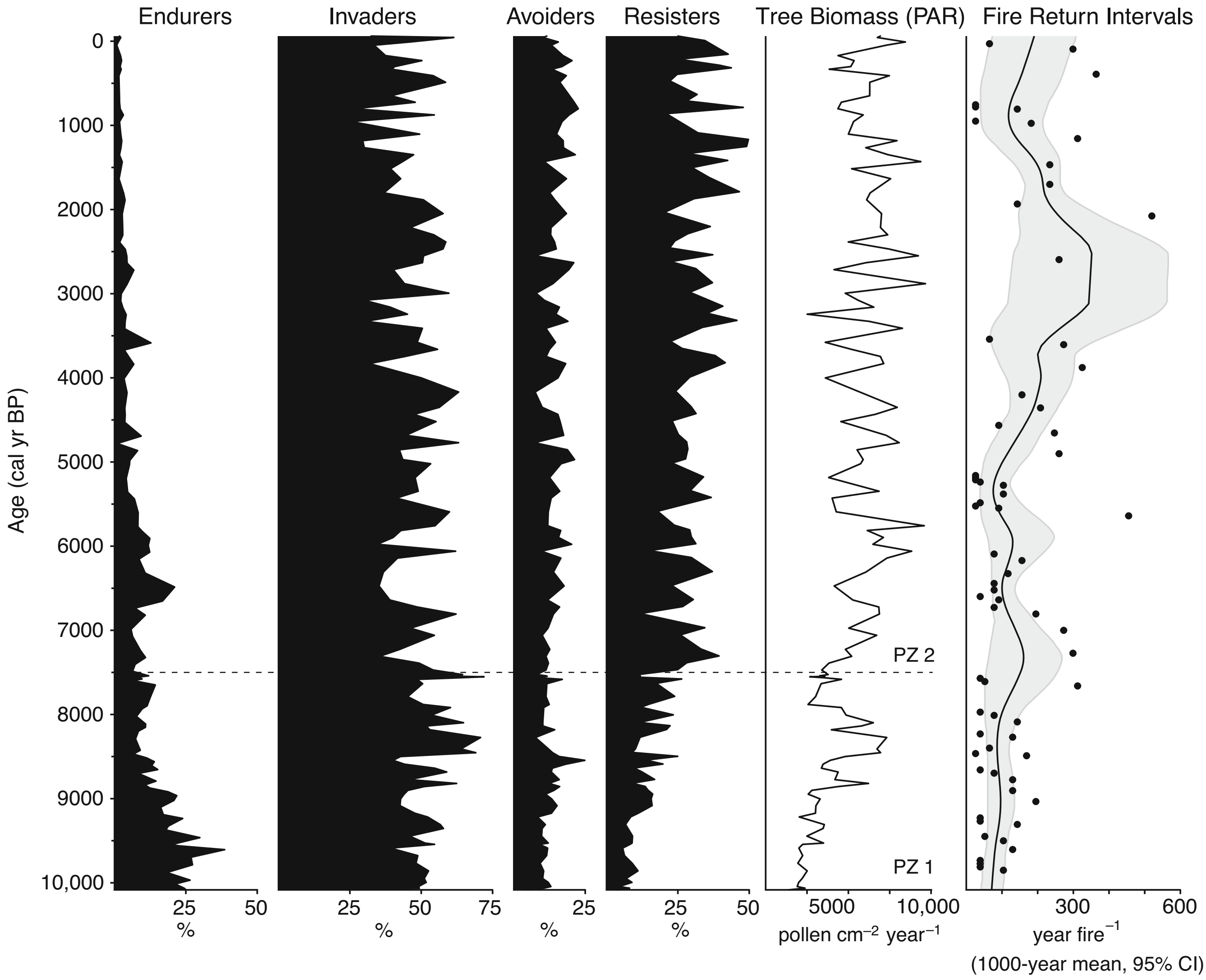

FIGURE 6 Relative abundance of fire endurers, invaders, avoiders, and resisters in the Roe Lake pollen record. Also shown are tree pollen accumulation rates (PAR) as a proxy for biomass and fire return intervals with 95% bootstrapped confidence intervals (CIs). Dashed horizontal line delimits pollen assemblage zones (PZs) based on cluster analysis. cal yr BP, calendar years before present.

a fire regime characterized by moderate severity fires every 100 years, on average. Although *P. menziesii* was already the most common conifer at the time, forests also included *P. contorta* and were more open than they are today with a large diversity of shrubs, herbs, and ferns in the pollen record and *P. aquilinum*, a fire promoting fern, dominating the understorey (Figure 5). Fire-adapted taxa including endurers were common during the early Holocene and tree PAR suggest that available fuel was low relative to the mid- and late Holocene (Figure 6). High prevalence of fire-adapted taxa is also seen elsewhere in the Pacific Northwest in the early Holocene. For example, Long et al. (2007) note a similar trend in the Coast Range of western Oregon (sites "X" and "AB" in Figure 1) when conditions were drier and fire was more frequent. The early Holocene mean fire frequency of 10 peaks 1000 year^{-1} at Roe Lake is consistent with charcoal records from other low-elevation locations in the Pacific Northwest with forests similar to the open-canopy *P. menziesii* forests near Roe Lake (e.g., Brown & Hebda, 2002b; Brown et al., 2019; Cwynar, 1987; Long et al., 2007). However, this early Holocene period of frequent fire also occurred in other forest types in the Pacific Northwest (e.g., Brown & Hebda, 2002b; Gavin et al., 2013, 2001; Hallett et al., 2003; Long et al., 2011; Prichard et al., 2009; Walsh et al., 2008; White et al., 2015).

At ~7300 cal yr BP, there is a notable increase in *Q. garryana* pollen at Roe Lake and by 6500 cal yr BP, *Q. garryana* accounts for 16% of the pollen assemblages (Figure 5). Nearby pollen records on Vancouver Island (e.g., Brown et al., 2022, 2019; Pellatt et al., 2001) show similar increases in *Quercus*, reflecting the establishment of Garry oak savanna communities throughout the region. At this time, fires continue to be frequent on Pender

Island with fires occurring, on average, every 101 ± 29 years between 7300 and 6000 cal yr BP. However, charcoal peak magnitudes are an order of magnitude lower relative to the early Holocene (Figure 4), suggesting the fire regime shifted to one characterized by smaller and/or lower intensity surface fires (Figure 4). The inference of a shift to lower intensity surface fires is consistent with modern observations of fire in *Q. garryana* ecosystems, which tend to be of low duration and intensity (Agee, 1993). At Battle Ground Lake in southwestern Washington ("Y" in Figure 1), ~330 km south of Pender Island, Walsh et al. (2008) note a similar shift in fire regimes to frequent episodes of low-to-moderate severity with abundant grass charcoal in association with *Quercus*-dominated savanna. At other paleoecological sites in the region, *Q. garryana* was also more abundant during periods of more frequent fire (Brown et al., 2019; Walsh et al., 2010). Although *Q. garryana* is considered a fire endurer, it exhibits both endurer and resister traits. Seedlings have deep taproots that allow for resprouting following fire and mature adults can have thick fire-resistant bark (Agee, 1993; Nemens et al., 2019). *Quercus garryana* seedlings are also often found on frequently disturbed sites along with other early successional taxa (Agee, 1993). These adaptations allow *Q. garryana* to outcompete many other woody species in environments with frequent low-severity fire, particularly *P. menziesii* (Nemens et al., 2019; Sprenger & Dunwiddie, 2011). Therefore, *Q. garryana* and its associated savanna communities on Pender Island would have benefitted from frequent low-severity fire by hindering *P. menziesii* encroachment. It is noteworthy that the decrease in *Quercus* abundance 5900–5500 cal yr BP coincides with a 450-year fire-free period. Less frequent fire would have allowed *P. menziesii* to eventually outcompete *Q. garryana* on Pender Island.

Forests on Pender Island in the mid- and late Holocene were *P. menziesii*-dominated closed-canopy forests. Decreased plant richness through this interval is indicative of decreased disturbance and PARs suggest tree biomass was generally higher, which would have increased the available fuel load (Figures 5 and 6). Fire regimes after 6000 cal yr BP are characterized by less frequent fire and therefore longer FRIs, relative to those in the early Holocene. The mean FRI lengthens to 176 ± 54 years, but return intervals vary considerably, reaching 350 years between 3000 and 2500 cal yr BP before fire frequencies increase over the last 2000 years. The shift toward less frequent fire in the mid-Holocene is typical of many sites in the Pacific Northwest, especially those with abundant *P. menziesii* (e.g., Brown et al., 2022, 2019; Long et al., 2007; Walsh et al., 2008). Sites to the north of Pender Island such as Somenos Lake on Vancouver Island ("F" in Figure 1; Murphy et al., 2019) and to the south in western Oregon, such as Lake Oswego ("Z" in Figure 1; Walsh et al., 2018) and Lost and Little lakes ("X" and "AB" in Figure 1; Long et al., 2007), also show a late Holocene increase in fire frequency similar to Roe Lake.

On Pender Island, longer FRIs in the mid-Holocene are associated with the fire resister functional type (i.e., *P. menziesii*) and would have hindered fire endurers such as *Q. garryana* and *P. aquilinum* that were common earlier in the record (Figure 6). Less frequent fire would have also facilitated the subtle increase in fire avoiders such as *T. heterophylla* (Figure 5), which tend not to establish in environments that frequently burn (Agee, 1993). Similar mid-Holocene increases in fire-sensitive taxa in western Oregon are also highlighted by Long et al. (2007). Feurdean et al. (2020) conducted a study similar to ours that compared long-term fire history to pollen-inferred plant functional types in western Siberia, where modern forests are also dominated by fire resister taxa. They found a comparable pattern of increasing resister and avoider functional types in association with low fire frequencies in the mid- to late Holocene.

The Roe Lake charcoal record indicates not only less frequent fire in the mid- and late Holocene, but also a shift to a fire regime characterized by mixed severity. Low- to moderate-magnitude charcoal peaks typically occur every ~150 years and these are interspersed with infrequent large-magnitude peaks that occur every ~500–2000 years, usually after long fire-free periods (Figure 4). This suggests a mixed fire regime of low-moderate-intensity fires of moderate frequency combined with infrequent crown or stand-replacing fires. This compares well with historical tree ring and fire scar records and analyses of age structures in *P. menziesii* forests in Washington and Oregon (Agee, 1993), which suggest a mixed fire regime of frequent low- to moderate-severity fires combined with infrequent stand-replacing fires. A similar mixed-severity fire regime with short cycles of low-intensity fires and long cycles of stand-replacing fires is also observed in boreal Siberia, where forests are also dominated by fire resister taxa, that is, *Larix sibirica* and *Pinus sylvestris* (Wirth, 2005).

Climate as the main driver of Holocene fire frequency

Climate acts as an overarching control on biomass burning on long timescales, with fire activity increasing with increased temperature (Daniau et al., 2012). On Pender Island, climate has regulated fire regimes for much of the last 10,000 years, both directly, with climatic trends generally correlating with trends in the charcoal record, and indirectly, through climate-driven shifts in forest composition and structure. In the early Holocene, warm, dry climate with high seasonality in association with a strengthened subtropical high-pressure system in the northeastern Pacific Ocean (Bartlein et al., 1998; Berger & Loutre, 1991; Heusser et al., 1985) created conditions conducive to more frequent fire (Figure 7). The mean FRI at Roe Lake was at its shortest in the warm and dry early Holocene with a mean FRI of 100 ± 27 years and as little as 26 years between fire episodes (Figure 4). As temperatures and moisture deficits decreased in the mid-Holocene in association with intensification of the Aleutian low-pressure system (Bartlein et al., 1998; Heusser et al., 1985; Nagashima et al., 2022), fire frequency decreased to a mean FRI of 176 ± 54 years. Relatively short-lived variations in climate, such as the Medieval Climate Anomaly and the Little Ice Age, are not visible in the Roe Lake record presented here, due to the 1000-year smoothing window. However, a 200-year long smoothing window imposed on the last 1300 years of the Roe Lake charcoal record revealed a mean FRI of 50 years during the warm and dry Medieval Climate Anomaly followed by longer return intervals (~125 years) only a few centuries later, during the colder and wetter Little Ice Age (Lucas & Lacourse, 2013).

Despite the overall pattern of reduced fire frequency in the mid- and late Holocene, wildfire episodes increased at Roe Lake between ~2000 and 1000 cal yr BP, a shift also seen in various forest types at other sites in southern BC (e.g., "F" in Figure 1; Murphy et al., 2019, "M" and "N" in Figure 1; Hallett et al., 2003) and elsewhere in the Pacific Northwest (e.g., "W," "X," and "AB" in Figure 1; Long et al., 2007). Most macroscale paleoclimate reconstructions do not suggest conditions conducive to more frequent fire during this time; however, nearby records of mean July air temperature (Lemmen & Lacourse, 2018) and sea-surface temperature (Kienast & McKay, 2001) do suggest subtle increases in temperature 2500–1500 cal yr BP (Figure 7). Warm El Niño–Southern Oscillation (ENSO) events are generally more common in the late Holocene (Moy et al., 2002) and this may have led to more frequent summer droughts. However, the relationship between

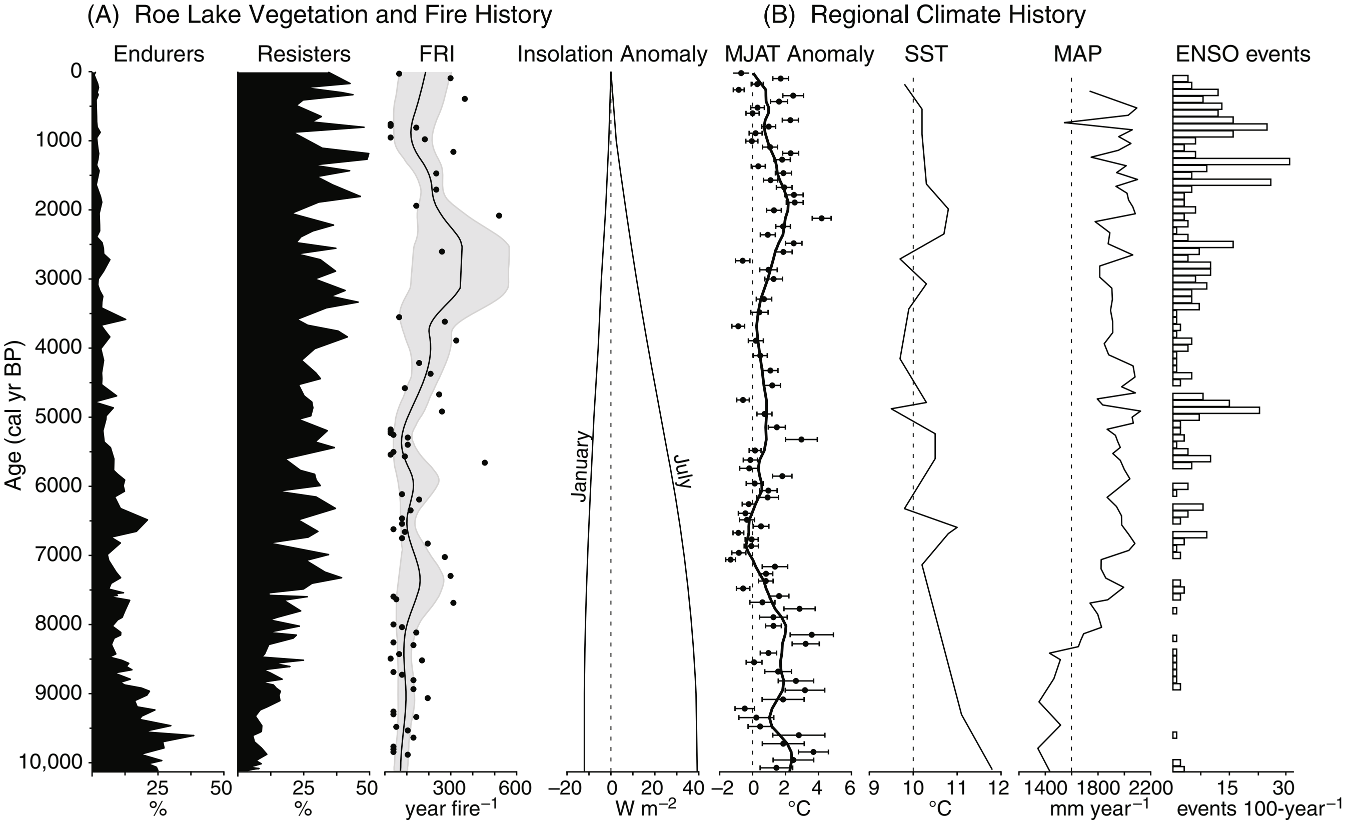

FIGURE 7 (A) Summary of Roe Lake vegetation and fire history, showing endurers, resisters, and fire return intervals (FRIs) with 1000-year mean and 95% bootstrapped confidence intervals in gray. (B) Independent paleoclimate proxies: January and July insolation anomalies at 50° N (Berger & Loutre, 1991); chironomid-inferred mean July air temperature (MJAT) anomalies at 49° N (Lemmen & Lacourse, 2018) with locally weighted scatterplot smoothing (LOWESS); alkenone-inferred sea-surface temperatures (SSTs) at 49° N (Kienast & McKay, 2001); pollen-inferred mean annual precipitation (MAP) for coastal British Columbia (Heusser et al., 1985); and number of warm El Niño–Southern Oscillation (ENSO) events in 100-year bins (Moy et al., 2002). cal yr BP, calendar years before present.

warm ENSO events and fire on long timescales remains unclear, with contradictory findings among studies (Walsh et al., 2015).

Human use of fire may well have also played a role in modulating fire regimes on Pender Island, especially in the late Holocene. Intentional burning by Indigenous peoples would have altered the timing, frequency, and distribution of fire, which may have also affected fuel structure and availability, at least at fine spatial scales (McCune et al., 2013). Studies on southern Vancouver Island and elsewhere in the Pacific Northwest commonly find more frequent fires in the late Holocene, despite a generally cool, wet climate, suggesting that intentional burning by Indigenous peoples may have had region-wide effects (Hoffman et al., 2016; Murphy et al., 2019; Walsh et al., 2018, 2017, 2015). Brown and Hebda (2002a) describe estimates of human populations in the southern Vancouver Island region ranging anywhere from a few hundred to 9000 people prior to European contact. Fire was used regularly by Indigenous peoples as a resource management tool (e.g., to promote the growth of plant foods such as *Camassia* bulbs), without igniting the forest canopy or causing stand-replacing fires (Lepofsky & Lertzman, 2008; Turner, 1999). Oral histories indicate that fire was also used to facilitate hunting and travel by creating open corridors and enhancing grasses for grazing by herbivores (Derr, 2014; Turner, 1999). Archeological and paleoecological evidence including increased charcoal accumulation and the presence of multihouse settlements suggests active fire management practices by Indigenous peoples in coastal BC by 5000 cal yr BP (Derr, 2014; McCune et al., 2013). Archeological studies document Indigenous populations on Pender Island starting ~5000 cal yr BP (Carlson et al., 2017; Ewonus et al., 2020), making human use of fire a possible source of ignition in addition to lightning. However, few archeological sites have been investigated on Pender Island, and the extent and duration of human occupation are mostly unknown. Thus, it is not possible to attribute the late Holocene increase in fire frequency to cultural practices. Furthermore, fires set by Indigenous peoples for cultural and/or ecological purposes would not likely have been large or intense enough (e.g., stand-replacing fires) to produce significant peaks in lake sediment charcoal records, rendering it difficult to differentiate these human-set fires from natural variability in background charcoal (Derr, 2014; Higuera et al., 2005; McCune et al., 2013).

CONCLUSION

The pollen and charcoal records from Pender Island reveal high functional diversity of fire adaptation combined with varying fire regimes over the last ~10,000 years. Climate and vegetation reconstructions are largely consistent with shifts in fire frequency, with warmer and drier summer climate in the early Holocene corresponding with high charcoal accumulation and moderate severity fires every ~100 years. At this time, plant communities were characterized by open *P. menziesii* forests with high diversity including an abundance of endurer taxa (e.g., *P. aquilinum*, *Q. garryana*) that have a competitive advantage in regimes of frequent fire. In the middle and late Holocene, cooler, wetter conditions with decreased seasonality were generally associated with longer FRIs and mixed-severity fires that allowed *P. menziesii*, the only true fire resister in the Roe Lake pollen record, to dominate forests and for fire avoiders to gradually become more common forest constituents. A period of more frequent fire around 2000 cal yr BP may be linked to more frequent summer droughts associated with ENSO events and/or intentional fires that were a component of resource management practices by Indigenous peoples. High-severity fire episodes are infrequent throughout the record and generally only occurred after long periods without fire due to fuel buildup over time.

With future warming (Wang et al., 2016), the range of *P. menziesii* is likely to expand northward and upslope on a regional scale (Brown et al., 2022; Halofsky et al., 2018; Lacourse & Adeleye, 2022; MacKenzie & Mahony, 2021). Elevated temperatures and more intense summer drought will decrease fuel moisture content in the abundant fuel conditions that have been created by fire exclusion and suppression (Abatzoglou & Williams, 2016; Hagmann et al., 2021). In turn, fire regimes are likely to be driven beyond the historical range of natural variability with larger, more frequent, and more severe fires, and longer fire seasons (Abatzoglou & Williams, 2016; Flannigan et al., 2005; Haughian et al., 2012). This enhanced fire activity is likely to favor *P. menziesii* and may well displace fire avoiders at both low (e.g., *T. heterophylla*) and high (e.g., *Tsuga mertensiana*) elevations (Lacourse & Adeleye, 2022; MacKenzie & Mahony, 2021). As summer climate continues to warm and dry, identified FRIs, particularly those of the warm and dry early Holocene, may be informative in the development of fire management strategies such as prescribed burning (Kelly et al., 2020; North et al., 2021). However, using prescribed burning as a management tool may become more difficult as fire seasons lengthen, as this will narrow the interval when conditions are not too moist or too dry to conduct controlled burns effectively and safely. Our study demonstrates clear linkages between changes in climate, fire regimes, and fire-related plant traits on long timescales. Given the intensification of fire activity expected across western North America, land managers should explicitly consider fire-related plant traits in conservation, restoration, and reforestation plans (Harrison et al., 2021). A trait-based approach can be used to assess forest resilience at stand and landscape levels and aid in the selection of species and phenotypes that enhance fire resilience (Moris et al., 2022; North et al., 2021).

ACKNOWLEDGMENTS

We thank M. Pellatt, J. Lucas, B. Hodgin, and T. Rodengen for help in the field, J. Lucas for help with pollen and charcoal analyses, and D. G. Gavin and J. A. Antos for constructive feedback on the research. This research was supported through research grants to Terri Lacourse from the Natural Sciences and Engineering Research Council of Canada (Grant no. 342003), Canada Foundation for Innovation (Grant no. 17214), British Columbia Knowledge Development Fund (Grant no. 804365), and Pacific Institute for Climate Solutions (Grant: *Understanding Ecosystem Responses to Climate Change in Southwestern British Columbia Forests*).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Charcoal, pollen, ^{14}C, and ^{210}Pb data and associated metadata are available from the Neotoma Paleoecology Database: https://doi.org/10.21233/jnyr-4x96.

ORCID

Terri Lacourse https://orcid.org/0000-0002-7559-5374

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Giuliano, Camille, and Terri Lacourse. 2023. "Holocene Fire Regimes, Fire-Related Plant Functional Types, and Climate in South-Coastal British Columbia Forests." *Ecosphere* 14(2): e4416. https://doi.org/10.1002/ecs2.4416