Old-growth forest structure in a low-productivity hypermaritime rainforest in coastal British Columbia, Canada

Kira M. Hoffman [ID],[1,2,3,4,†] Brian M. Starzomski,[1,2] Ken P. Lertzman,[1,5] Ian J. W. Giesbrecht,[1,5] and Andrew J. Trant[1,2,4]

[1]Hakai Institute, P.O. Box 309, Heriot Bay, British Columbia V0P 1H0 Canada
[2]School of Environmental Studies, University of Victoria, 3800 Finnerty Road, Victoria, British Columbia V8P 5C2 Canada
[3]Bulkley Valley Research Centre, P.O. Box 4274, Smithers, British Columbia V0J 2N0 Canada
[4]School of Environment, Resources and Sustainability, University of Waterloo, 200 University Avenue West, Waterloo, Ontario N2L 3G1 Canada
[5]School of Resource and Environmental Management, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6 Canada

Abstract. Dendrochronological analyses were conducted across a gradient of productivity and soil drainage quality characterizing four vegetation types in a low-productivity hypermaritime (perhumid) temperate rainforest on the Central Coast of British Columbia, Canada. We examined the structure, composition, and stand dynamics of trees growing in 400 m^2 plots located in blanket bog, bog woodland, bog forest, and zonal forest vegetation types. We sampled over 2500 trees and 1500 seedlings and saplings and our dendrochronological reconstruction of six tree species revealed establishment ages extending to 660 A.D. (1350 yr). All forest plots contained numerous old trees (>250 yr) and the zonal forest and bog forest vegetation types contained significantly taller trees and also had the greatest amount of suppressed, shade-tolerant tree species. The bog woodland vegetation type contained more seedlings and saplings than the other three vegetation types combined. The bog forest vegetation type had the highest density of dead standing trees (~530 per hectare). Blanket bogs contained an open structure with very few old trees (>250 yr). Significant differences in the ages of trees existed between forested vegetation types and the more open blanket bog vegetation type. Several trees exceeded 1000 yr in age and were situated in lower-productivity bog forest and bog woodland sites. We found no evidence of widespread tree cohort establishment, indicating that small-scale disturbances such as individual tree mortality and gap-forming dynamics are likely the most frequent disturbance in the study area.

Key words: British Columbia; coastal temperate rainforests; dendrochronology; disturbance history; ecosystem plots; forest mensuration; forest stand dynamics; forest structure; hypermaritime; muskeg; old-growth forests; perhumid temperate rainforests.

† **E-mail:** khoff@uvic.ca

Introduction

Natural and anthropogenic disturbances occur across temporal and spatial scales and play an important role in forest ecosystem dynamics (Pickett and White 1985, Turner 1989, White et al. 2018). Although large-scale disturbances such as wind, fire, and insect outbreaks characterize boreal and temperate interior forests in Western North America, temperate rainforest ecosystems

in the coastal temperate rainforest (CTR) of North America are generally dominated by small-scale, multicohort disturbances such as standing tree mortalities or single-tree fall (Spies and Franklin 1988, Lertzman 1992, Lertzman et al. 1996, Banner et al. 2005, Daniels and Gray 2006). Gap-forming disturbances as a result of tree mortality (standing dead or fallen trees) affect large portions of old-growth temperate rainforests annually, and millennia of these small-scale disturbances coupled with conifer adaptations to withstand disease and fungal pathogens have promoted old growth, multi-age forests across the northern CTR (Swanson and Franklin 1992, Lertzman et al. 1996, MacKinnon 2003, Daniels and Gray 2006, DellaSala et al. 2011, White et al. 2018). Meanwhile, small gap-forming disturbances interact with gap-forming edaphic conditions to create complex spatial gradients of canopy structure and developmental processes across landscapes and within stands (Lertzman et al. 1996). At the ecotone to non-forested landscapes of this region (e.g., subalpine parkland), edaphic and climatic controls become more important than gap processes (Brett and Klinka 1998). Much less is known about the interplay of gap and edaphic processes at the ecotone between forests and wetlands in the CTR.

British Columbia (BC) contains the largest and most intact CTR in the world, parts of which originally covered much of Vancouver Island, Haida Gwaii, and the central and north coast (Mackinnon 2003, DellaSala et al. 2011, Alaback et al. 2017; see Shackelford et al. 2018 for loss of CTR extent). While several studies examining old-growth forest characteristics and gap-forming dynamics have been carried out in warmer and drier rain shadow variants of temperate rainforests located in the Pacific Northwest of the USA (Spies and Franklin 1988, Spies et al. 1990), and in the tall productive (Lertzman et al. 1996, Frazer et al. 2000, Giesbrecht et al. 2017) and montane (Parish and Antos 2004) CTR forests of BC, major knowledge gaps remain for the short and slow-growing hypermaritime temperate rainforests located on the outer coast of BC (Kranabetter et al. 2003, 2013, Mackinnon 2003, Banner et al. 2005, Daniels and Gray 2006, LePage and Banner 2014). Similarly,

hypermaritime forests have been studied in Southeast Alaska (Alaback 1982, Buma et al. 2016, Bisbing and Amore 2018, Buma and Thompson 2019), but it is unclear if knowledge from Alaska's hemlock spruce-dominated forest stands are transferable to the cedar–hemlock stands of coastal BC.

Information on old-growth forest structure in hypermaritime temperate rainforests on the coastal margin of BC is scarce despite their importance for wildlife (Adams et al. 2017, Obrist et al. 2020, Service et al. 2020), soil carbon storage (McNicol et al. 2019), and exports of dissolved organic carbon (Oliver et al. 2017), which provide energy subsidies to marine environments (St. Pierre et al. 2020). These landscapes are characterized by mosaics of wetlands and short-open forests (Thompson et al. 2016) and are comprised of long-lived conifer species, yet little is known about species turnover, life histories, and disturbance regimes (Daniels and Gray 2006, Alaback et al. 2017; but see Banner et al. 1983 and LePage and Banner 2014). Forest attributes derived from highly resolved dendrochronological records are necessary to understand long-term ecological changes in temperate rainforests and infer complex interactions between vegetation and disturbances (Daniels and Gray 2006, Hoffman et al. 2017).

Reconstructing the rate of forest stand establishment, species distributions, and seedling regeneration across vegetation types and along gradients of productivity can assist with understanding both the dynamics and trajectories of old-growth forests (Mackinnon 2003, Alaback et al. 2017). Because of the persistently cool humid climate, many forested areas on the central and north coast of BC are characterized by thick organic soils on forest floors with slow rates of decomposition, poor nutrient cycling, and large accumulations of peat (Asada et al. 2003, Banner et al. 2005). Deterministic long-term succession from productive forests to lower-productivity bogs can no longer be assumed, as paleoecological proxies from peat bogs on Haida Gwaii in BC indicate that disturbances such as drought can cause productive forests to invade bog ecosystems (Banner et al. 1983, Huntley et al. 2013, Caouette et al. 2016). This dynamic relationship between forested and bog ecosystems is strongly influenced by allogenic factors such as

climate and local multi-scale disturbances (Klinka et al. 1996).

Our study addresses knowledge gaps and underlying assumptions of old-growth forest characteristics in a BC hypermaritime (perhumid) temperate rainforest. We use dendrochronology to reconstruct 1350 yr of stand establishment, forest structure, and forest composition across four vegetation types on the Central Coast of BC (Fig. 1). We conduct field sampling in permanent plots distributed across four dominant vegetation types (blanket bog, bog woodland, bog forest, and zonal forest) to address the following questions: (1) Are trees in the same age class (cohorts) present, and if so, do they indicate past plot-level disturbances? (2) What is the density and composition of living and standing dead trees? (3) How do tree species, size, and age vary across a landscape drainage gradient?

MATERIALS AND METHODS

Study area

The study area encompasses 20 km^2 on Calvert and Hecate Islands (North 51°39′ Latitude, West 128°04′ Longitude) within the Hakai Lúxvbálís Conservancy on the Central Coast of BC, Canada (Fig. 1). This part of the coastal margin of BC has many small islands characterized by exposed and rocky homogenous quartz diorite and granodiorite bedrock, subdued terrain, and elevations ranging from sea level to over 1000 m (Roddick 1996). Cool temperatures (average annual from 1943 to 2010 is ~7°C, average summer ~12°C) coupled with locally abundant (to ~4000 mm) and year-round rainfall distinguish this temperate climate region (Banner et al. 1993, 2005). The study area is located within the very wet hypermaritime subzone (CHWvh2) of the Coastal Western
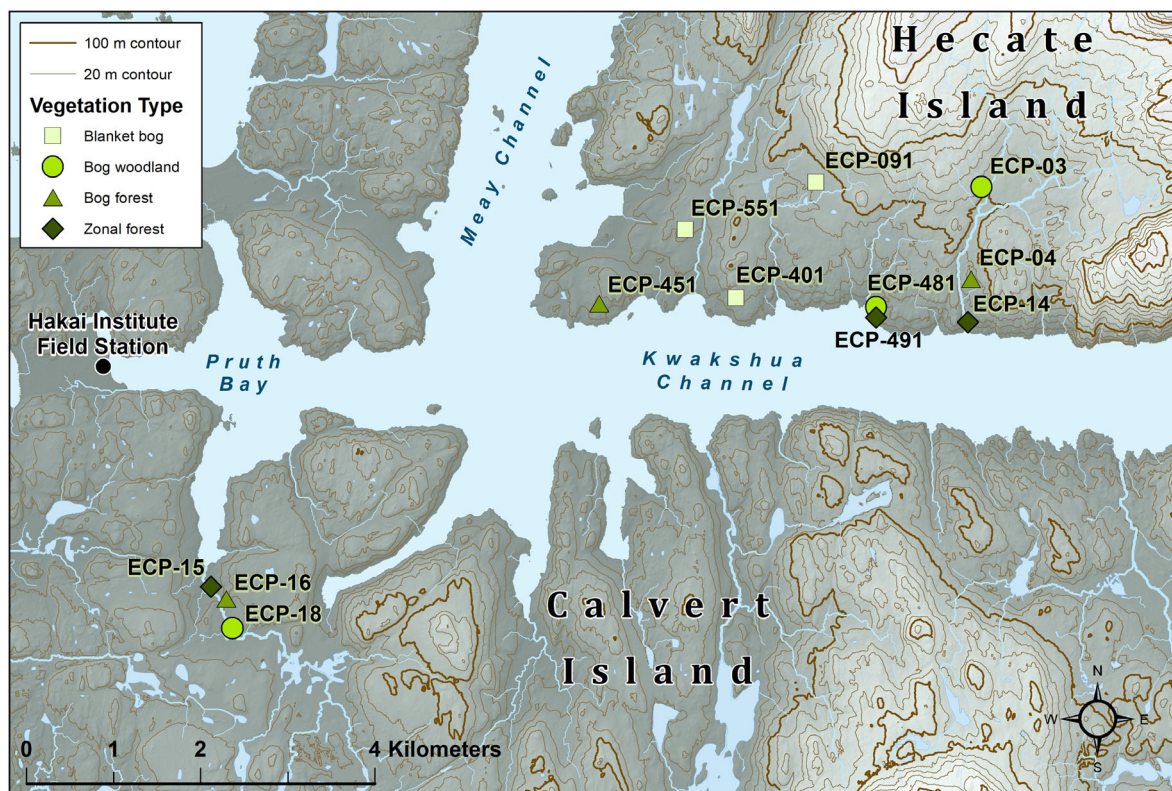

Fig. 1. The location of the 12 permanent ecosystem plots sampled across four vegetation types (blanket bog, bog woodland, bog forest, zonal forest; listed by increasing productivity) on Calvert and Hecate Islands located on the Central Coast of British Columbia, Canada.

Hemlock biogeoclimatic classification (Pojar et al. 1991).

Excess soil water regulates this environment and subtle variation in slope or drainage leads to significant differences in forest productivity, particularly on nutrient-poor sites with little soil disturbance (Banner et al. 2005, Kranabetter et al. 2013). Although several forested and non-forested vegetation types in this hypermaritime (perhumid) temperate rainforest have been described across the study area (Green 2014, Thompson et al. 2016), four vegetation types dominate along a gradient of productivity and are defined by species and closely associated landforms (Fig. 2; Banner et al. 1993, 2005). Blanket bogs (Fig. 2a; CWHvh2/32) are nutrient-poor, non-forested minerotrophic or ombrotrophic shallow bogs that contain small amounts of western redcedar (*Thuja plicata* Donn ex D. Don.), yellow-cedar (*Xanthocyparis nootkatensis* [D.Don] Farjon and Harder), and shore pine (*Pinus contorta var. contorta* Douglas ex Loudon; Banner et al. 1993). Bog woodlands (Fig. 2b; CWHvh2/12) are the wettest forested sites and consequently have a sparse tree cover (Banner et al. 1993). These forests contain roughly equal densities of western redcedar, yellow-cedar, and shore pine with lesser amounts of mountain hemlock (*Tsuga mertensiana* [Bong.]; Klinka et al. 1996). Bog forests (Fig 2c; CWHvh2/11; Banner et al. 2005) are found on wet sites and exhibit more stunted growth forms dominated by western redcedar, yellow-cedar, western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and shore pine (Klinka et al. 1996). Zonal forests (Fig. 2d; CWHvh2/01) are characterized as being open and scrubby because of the hypermaritime climate (Banner et al. 1993) yet represent comparatively productive stands for this study area. They are imperfectly drained sites found in both hillslope and valley-bottom locations with comparatively large-diameter western redcedar and western hemlock and lesser amounts of yellow-cedar and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) (Pojar et al. 1991).

Field sampling

Terrestrial ecosystem maps and satellite imagery taken in 2012 were used to select the locations of 12 permanent plots (11.28 m radius, 0.04 ha) with a stratified random sampling design representing the four vegetation types on Calvert and Hecate Islands (Fig. 1). The 12 plots contained no visible aboveground or below-ground evidence of recent stand-replacing disturbances (fire, wind, mass wasting) or documented historical resource management by First Nations (culturally modified trees, shell middens, fire, land clearing). Plots were selected to represent a relatively uniform site without strong topographic or edaphic variation within plot boundaries.

In all plots two, 5 mm diameter increment cores were sampled from the bases (~15 cm height) and two from the breast height (~1.3 m) of all trees >7.5 cm diameter at breast height (dbh). Tree cores were sampled from bark to pith perpendicular to the slope to avoid reaction wood (Speer 2010). The dbh of all trees was measured at 1.3 m from the tree base and the tree height, tree species, and tree health were also recorded. The age of trees, density of stems per hectare, dbh, and presence of dead standing trees were sampled to define old-growth characteristics in each plot. In addition, the density of stems per hectare of all shade-tolerant and shade-intolerant trees was used to assess the relationship between tree height, dbh, and age (Oliver and Larson 1990). All saplings (<7.5 cm dbh, >15 cm height) and seedlings (<15 cm height) were characterized (by species, height, and dbh), counted, and then destructively sampled in five, 4-m^2 subplots. A diagram of how subplots were sampled is found in Appendix S1: Fig. S1.

Dendrochronological analyses

In the laboratory, tree cores (from trees >7.5 cm dbh) and sapling disks (from trees <7.5 cm dbh) were processed using standard dendrochronological techniques (Stokes and Smiley 1968). Samples were measured and counted using a Velmex sliding stage micrometer (precision 0.001 mm) and then statistically verified using the computer program COFECHA and R statistical software package dplR (Grissino-Mayer 2001, Bunn 2008, R Development Core Team 2016). For cores that did not reach pith, we used Duncan's (1989) method to calculate the distance to the chronological center of each tree. Tree whorls on seedlings (<15 cm height) were counted under a microscope in the

Fig. 2. Photographs of the four dominant vegetation types sampled on Calvert and Hecate Islands, British Columbia, Canada. These vegetation types are situated along a gradient of productivity and include (a) blanket bog, (b) bog woodland, (c) bog forest, and (d) zonal forest. Although the zonal forest vegetation type has the largest trees in height and diameter, the bog woodland and bog forest vegetation types contain the highest density of trees exceeding 1000 yr, the majority of which are under 3 m in height and less than 50 cm diameter at breast height.

laboratory to determine the seedling age and species.

The median age and height of saplings (<7.5 cm dbh and >15 cm height) from each tree species were used to estimate time to reach coring height for tree cores sampled from the root collar of every tree >7.5 cm dbh in each plot. For age structure analyses, we binned trees (>7.5 cm dbh) together by decade to reduce uncertainty in time to reach coring height (Tepley and Veblen 2015). We calculated the density per hectare of all seedlings, saplings, and trees by species and vegetation type. We compared the density of tree species (>7.5 cm dbh) across four dbh categories and six age classes in every plot along with the density of regenerating tree species (<7.5 cm dbh) by six age classes in each subplot (Appendix S1: Fig. S1).

Statistical analyses

To define fine-scale disturbances and associated growth events, we used a combination of radial growth averaging (Nowacki and Abrams 1997) on trees (>7.5 cm dbh) that comprised the contemporary canopy structure in zonal forest and bog forest vegetation types (Altman et al. 2014). We sampled trees that were at least 100 yr old to reconstruct fine-scale disturbances and understand growth trajectories of suppressed understory trees in the closed canopy zonal forest and bog forest vegetation types (Splechtna et al. 2005). Stand establishment data in each plot were compared to the average radial growth of recorder trees in the previous 10-yr period to assess growth releases in the R package TRADER (Altman et al. 2014). To account for interspecies differences, we only calculated release growth

thresholds within cross-dated species-specific chronologies and applied conservative 75% growth release criteria (Nowacki and Abrams 1997). We assessed sustained growth releases of at least 15 yr to identify canopy disturbances from the effects of favorable growing years associated with climate shifts (Nowacki and Abrams 1997). Synchronous growth releases were identified as at least three trees in each plot recording a sustained growth release.

There was strong evidence of non-normality and unequal variance in our raw data comparing tree age, height, and dbh. Therefore, we used a Kruskal–Wallis test, a rank-based non-parametric test to determine statistically significant differences between two or more groups using the statistics package pgirmess in R statistical software (R Development Core Team 2016, Giraudoux et al. 2018). We then used a Conover–Iman test to report the significance of multiple pairwise combinations (McDonald 2014).

We used a nested ANOVA within the five subplots sampled across the four vegetation types to compare differences in the ages of tree saplings and tree seedlings using the linear and non-linear mixed effects model package (nlme) in R statistical software (R Development Core Team 2016, Pinheiro et al. 2017). The site type (four vegetation types) represents a fixed factor at the top of the hierarchy and the sample type (five subplots) was the random nesting factor. Including subreplication of the samples in our hierarchical design reduced the unexplained variation and increased the power of the test for the main treatment effect (vegetation type). The data were aggregated and the linear mixed effects model was fit. The variance components of each random effect were assessed to verify the impacts of site and vegetation type. We calculated the 95% confidence intervals of the fixed effects (based on Markov chain Monte Carlo sampling) following the methods of Logan (2010).

RESULTS

Plot-level reconstructions

Our dendrochronological reconstruction of tree establishment reliably extended 1350 yr to the first recorded yellow-cedar tree in the year 660 in the bog forest vegetation type (Fig. 3). In total, we sampled 2500 trees to assess plot age

structure, radial growth patterns, and reconstruct fine-scale disturbances. All vegetation types contained multi-aged stands and old trees (>250 yr), but the average number of old trees was higher in the zonal forest, bog forest, and bog woodland vegetation types when compared to the blanket bog vegetation type (Fig 4). The combined density of old-growth trees (>7.5 cm dbh) across all vegetation types was approximately 170 stems per hectare (Fig. 5). Dendrochronological reconstructions of tree ages confirm that trees (>7.5 cm dbh) have persisted at densities of approximately 80 trees per hectare in the zonal forest vegetation type, 85 trees per hectare in the bog forest type, 95 trees per hectare in the bog woodland vegetation type, and 15 trees per hectare in the blanket bog vegetation type for at least 200 yr (Figs. 3, 5). The bog woodland vegetation type had the highest density of old trees (>250 yr) per hectare (~70 stems/ha; Fig. 5) and sixteen trees exceeded 1000 yr in age across the four vegetation types (Appendix S2: Table S1). Western redcedar and yellow-cedar trees comprised over 50% of the 2500 trees sampled across each plot (Fig. 5).

Growth release and regeneration

Multiple synchronous growth releases (three or more trees recording >75% sustained growth over a 15-yr period) were documented in the zonal forest and bog forest vegetation types (Appendix S2: Table S2). Growth releases were cross-dated to four species-specific chronologies (western redcedar, yellow-cedar, western hemlock, and mountain hemlock) and major growth release events (>75% increase in radial growth) occurred on average every 69 yr (median = 75 yr) years in the bog forest vegetation type and every 34 yr (median = 34 yr in the zonal forest vegetation type (Appendix S2: Table S2). The recruitment of overstory trees within the forest canopy has been relatively constant in the zonal and bog forest vegetation types since 1500 (Fig. 3). Several tree cores sampled at the bases of trees could not be included in growth release analyses due to the presence of reaction wood formation and narrow ring widths from decades of understory suppression (Splechtna et al. 2005). Analyses of growth releases in Sitka spruce were not possible as growth was not inhibited in the favorable zonal forest vegetation type.
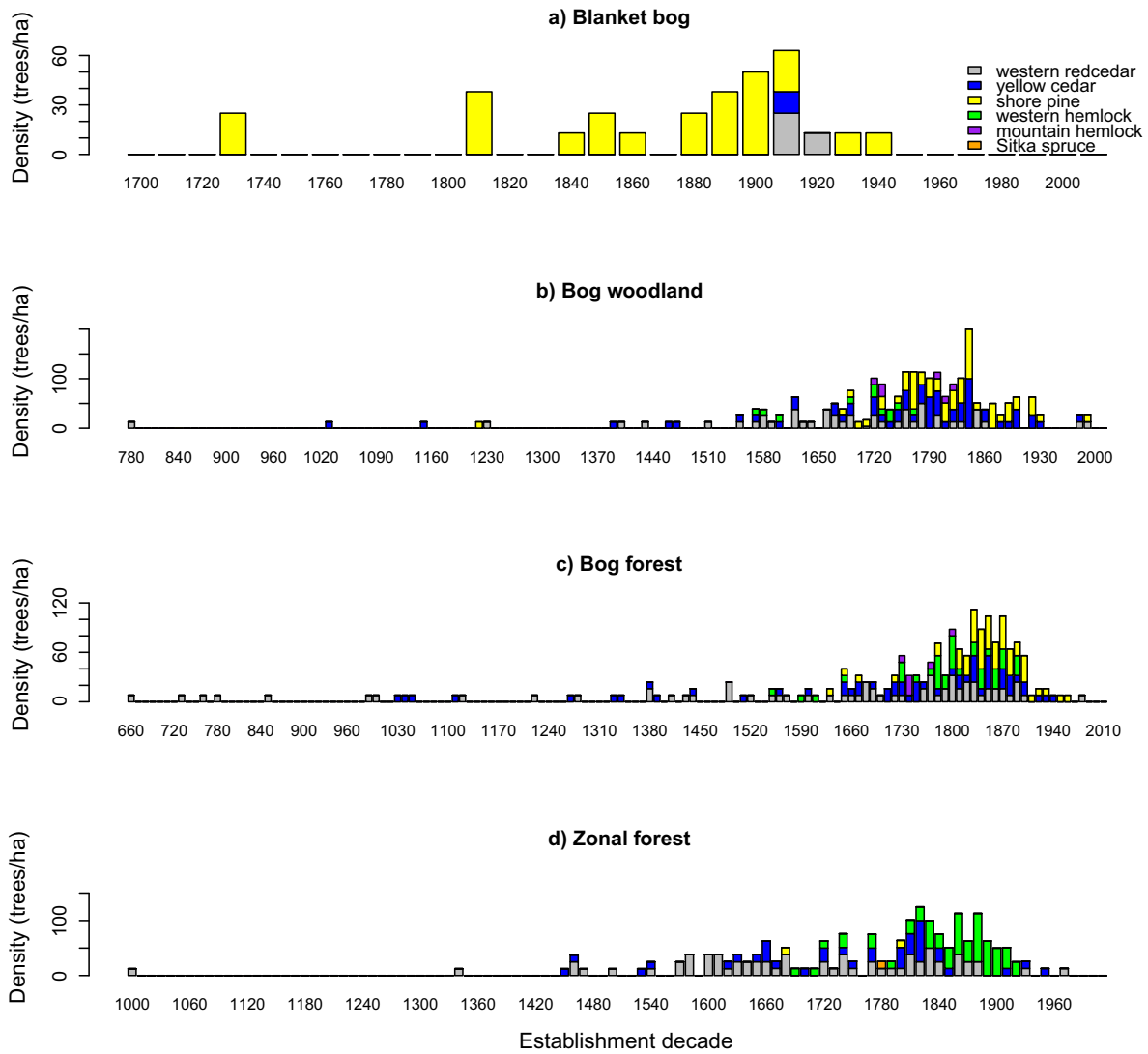
Fig. 3. The 1353 yr record (spanning 660–2013) of density of trees (>7.5 cm diameter at breast height) per hectare binned by decade of establishment across four vegetation types: (a) blanket bog, (b) bog woodland, (c) bog forest, and (d) zonal forest, sampled from 12 plots in the study area. Species are western redcedar (gray), yellow-cedar (blue), western hemlock (green), shore pine (yellow), Sitka spruce (orange), and mountain hemlock (purple). Note the different x and y axes provided for each subset figure.

Shade-tolerant western hemlock dominated the subcanopy and understory in the zonal forest type and western redcedar and yellow-cedar trees dominated the understory in the bog forest type. Western redcedar and yellow-cedar were the most common regenerating species in the bog woodland and bog forest vegetation types (Fig. 6). Shade-intolerant shore pine seedlings were mostly absent from the zonal forest vegetation type. The bog woodland vegetation type contained more saplings (<7.5 cm dbh) and seedlings (<15 cm height) than the other three vegetation types combined (~900 per hectare; Fig. 6), the majority of which were western redcedar. Seedlings and saplings growing in bog woodland vegetation plots were also significantly older (nested ANOVA: $F = 54.49$, df = 3, $P < 0.001$; Appendix S1: Fig. S2).
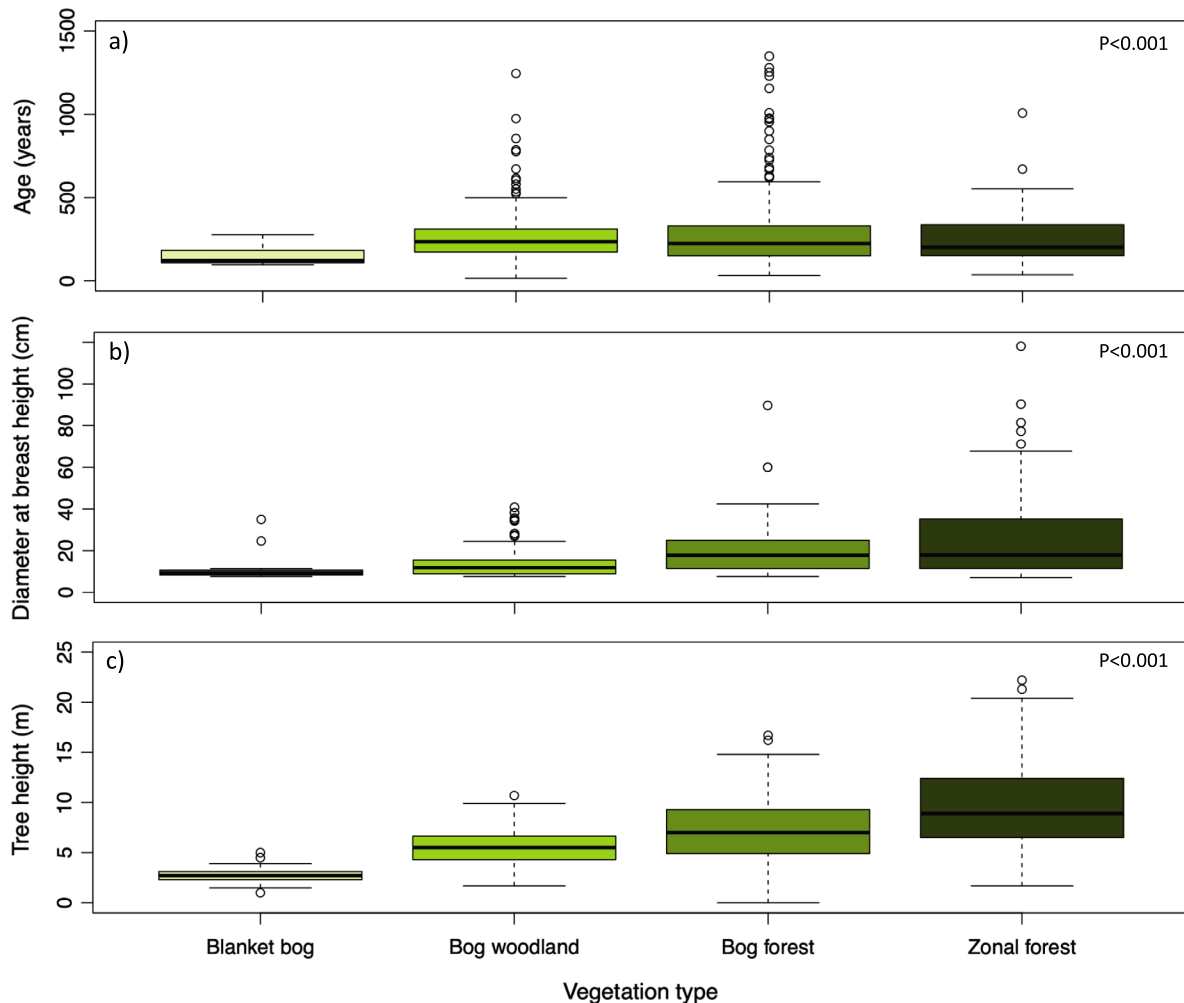
Fig. 4. Significant differences exist in (a) the age of trees >7.5 cm diameter at breast height (dbh) (b) trees >7.5 cm dbh, and (c) tree height in meters across the four vegetation types (blanket bog, bog woodland, bog forest, and zonal forest). Boxes represent the first and third quartile ranges, and the centerline is the median.

The zonal forest, bog forest, and bog woodland vegetation types contained approximately 10 times the density of trees >7.5 cm dbh when compared to the blanket bog vegetation type (Figs. 3, 5). The largest trees (tallest and greatest dbh) were found in the zonal forest vegetation type, and tree size and height decreased along the gradient to non-forested blanket bogs (Fig. 4; Appendix S1: Fig. S3). This is consistent with past results that show better soil drainage supports higher forest productivity in nutrient-poor hypermaritime forests (Kranabetter et al. 2003, Banner et al. 2005, Buma et al. 2016).

Multiple pairwise comparisons revealed significant differences between the median age of trees (>7.5 cm dbh) in the zonal forest, bog forest, and bog woodland vegetation types when compared to the median age of trees in the blanket bog vegetation type ($P = 0.001$; Fig. 4a). Significant differences also existed in the median dbh of trees >7.5 cm ($P = 0.001$; Fig. 4b) and the median height ($P = 0.001$; Fig. 4c) of trees across the four vegetation types. The age of regenerating trees (<7.5 cm dbh) also varied significantly across vegetation types, with the oldest regenerating trees found in bog woodlands and the youngest in
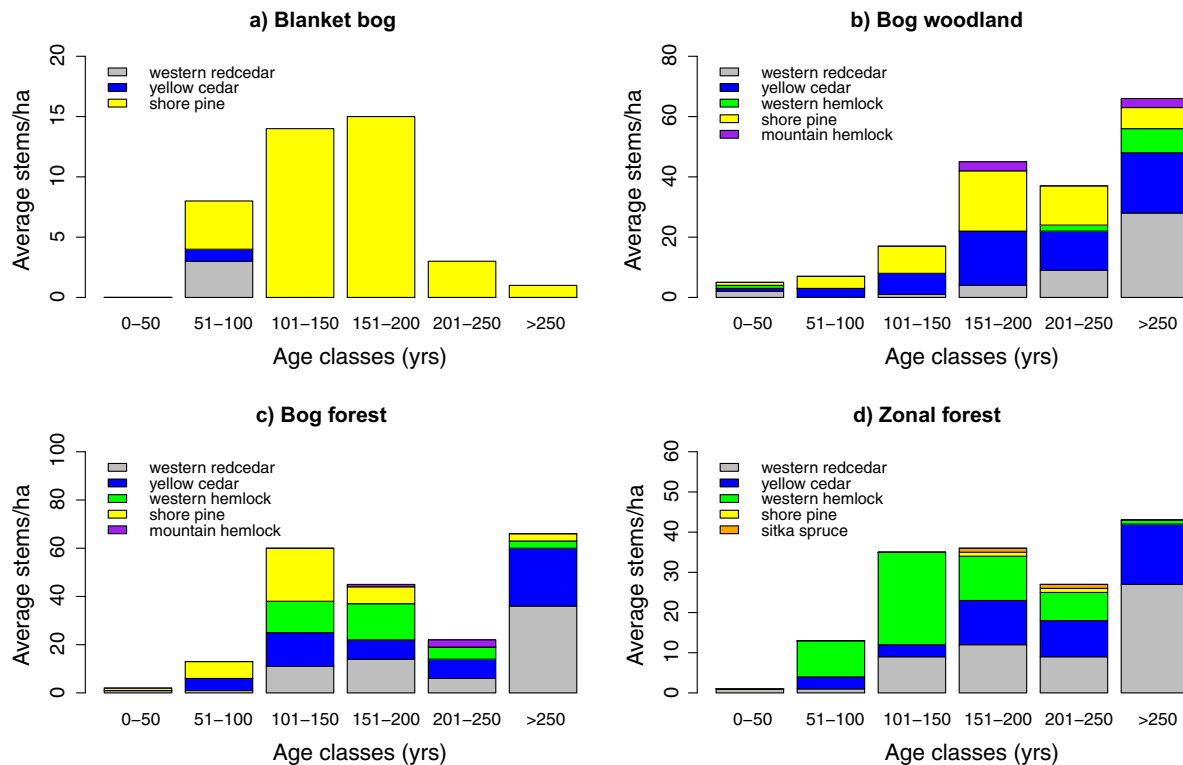
Fig. 5. Six age class distributions are described for trees >7.5 cm diameter at breast height sampled from 12 permanent plots on Calvert and Hecate Islands across four vegetation types: (a) blanket bog, (b) bog woodland, (c) bog forest, and (d) zonal forest. The density of stems per hectare is explained on the *y*-axis (note the difference axis scales). Old trees in this forest type are classified as greater than 250 yr. Species are western redcedar (gray), yellow-cedar (blue), western hemlock (green), shore pine (yellow), Sitka spruce (orange), and mountain hemlock (purple).

blanket bogs (Fig. 6). The zonal forest, bog forest, and bog woodland vegetation types contained approximately 30 old trees (>250 yr) per hectare (Fig. 3). Blanket bogs contained very few old trees, all of which were very small (<3 m height), and were comprised of only three tree species compared to the other vegetation types with up to six tree species present (Appendix S2: Table S1).

Density and composition of standing dead trees

Average densities of standing dead trees per hectare were 400 stems per hectare in the zonal forest vegetation type, 530 in the bog forest vegetation type, 380 in the bog woodland vegetation type, and 60 in the blanket bog vegetation type (Appendix S2: Table S1). Dead trees comprised over 28% of the overstory canopy in the zonal forest and bog forest vegetation types, and 90% of dead trees sampled were rot-resistant western redcedar and yellow-cedar. The majority of

standing dead trees could not be accurately aged, nor time of death dated due to heart rot and overall wood decay.

DISCUSSION

In this study, we examined the structure, composition, and stand dynamics of low-productivity hypermaritime temperate rainforests and wetlands on the Central Coast of BC. Our dendrochronological analyses sampled across four vegetation types characterized by a gradient of productivity revealed: (1) Forests were all multi-age stands indicating fine-scale mortality events are the most common disturbance type, (2) rot-resistant standing dead western redcedar and yellow-cedar trees were commonplace, (3) tree size increased along the drainage gradient from blanket bogs to zonal forests, (4) the age, density, and species of trees regenerating were related to
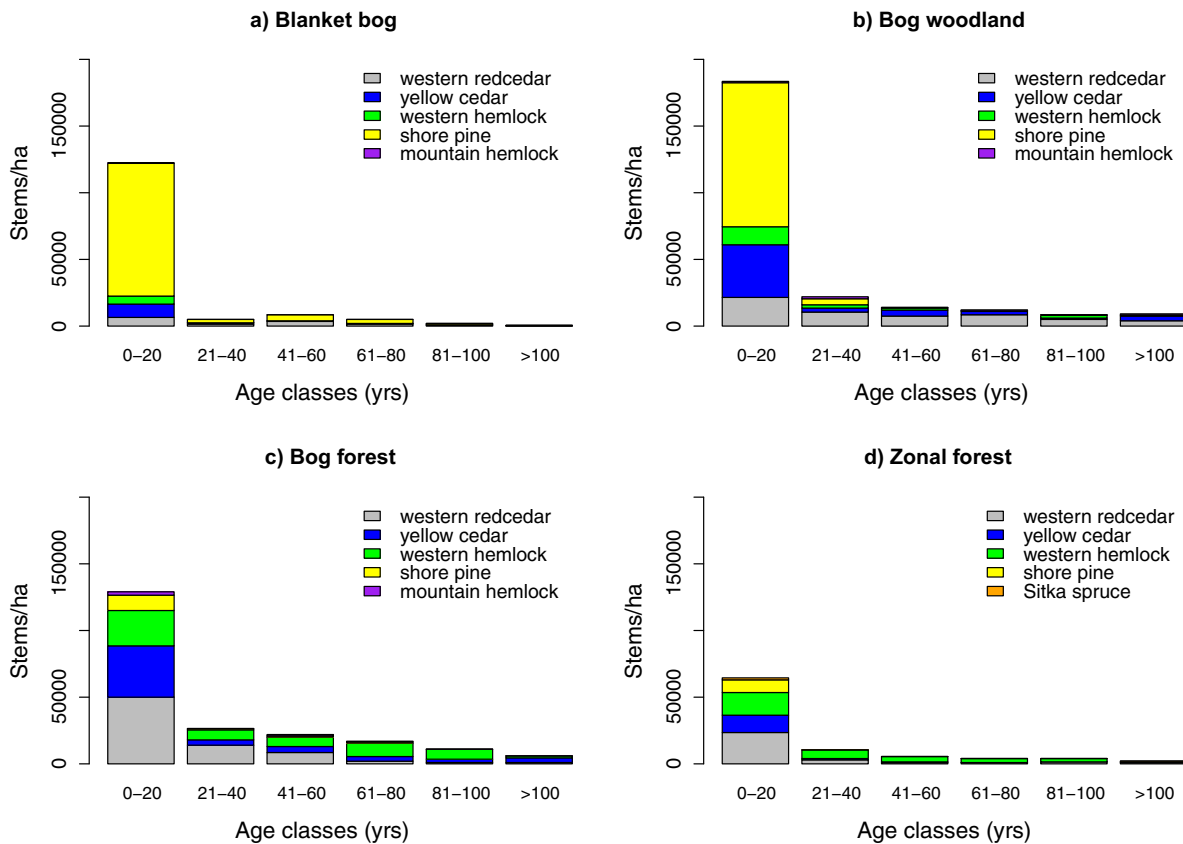
Fig. 6. The average number of regenerating seedlings and saplings (<7.5 cm diameter at breast height) sampled from 12 permanent plots in each of the four vegetation types vegetation types (blanket bog, bog woodland, bog forest, and zonal forest) on Calvert and Hecate Islands. Species are western redcedar (gray), yellow-cedar (blue), western hemlock (green), shore pine (yellow), Sitka spruce (orange), and mountain hemlock (purple). The density of stems per hectare is presented on the *y*-axis.

disturbance and life-history characteristics, and (5) old-growth trees were characterized by a range of heights and diameters, and legacy trees (those exceeding 1000 yr) were most common in the bog forest and bog woodland vegetation types.

We found no evidence of stand-replacing disturbances resulting in cohort establishment across the four vegetation types. This indicates that fine-scale disturbances such as single-tree fall or standing dead trees are likely the most common disturbance type in the study area, similar to more productive landscapes of the CTR (Lertzman et al. 1996). The zonal forest and bog forest vegetation types contained complex canopy structure, and all vegetation types contained trees of uneven age and size. According to applied disturbance regime theory,

forests with old trees accounting for approximately 50% of forest cover should experience stand-initiating (replacing) disturbances at intervals of ~350 yr (Biodiversity Guidebook 1995). Using a mean interval of 350 yr almost certainly underestimates the period between stand-replacing disturbances in CTR; large-scale, stand-replacing disturbances such as lightning-caused fires and wind events are likely to be much less frequent (Daniels 2003, Daniels and Gray 2006).

Tree species composition varied across vegetation type, likely due to differences in light, soil water and pH, nutrients and life-history traits, and tree physiology (Banner et al. 1993, 2005). Western redcedar and yellow-cedar are highly rot-resistant and dead trees may stand for decades to centuries (Hennon and Loopstra 1991,

Daniels et al. 1997). Similar to the effects of single-tree fall, senescence of long-lived western redcedar and yellow-cedar trees can promote pulses of regeneration and growth releases in light-limited stands even though the tree remains standing (Ott and Juday 2002). Light requirements are important for tree species during establishment, and many rainforest species utilize forest gaps and nurse logs from single-tree fall events to regenerate from seed (Modrzyński et al. 2015; Appendix S1: Fig. S4). In the hypermaritime forests of BC, these canopy-controlled processes likely decrease in importance along the edaphic (drainage) gradient from zonal forests to blanket bogs where edaphic controls predominate in the absence of dense tree cover.

In the zonal forest vegetation type, which has the greatest canopy cover, shade-tolerant western hemlock seedlings were abundant on nurse logs and saplings formed thickets, though regeneration of western redcedar and yellow-cedar saplings (>15 cm height), both considered shade-tolerant, was scant. This suggests that western hemlock may be more shade tolerant or have greater physiological plasticity than western redcedar and yellow-cedar. Alternatively, western hemlock regeneration may be favored by greater abundance of nurse logs in this vegetation type and by greater production of large-winged seeds that can be dispersed over long distances (between 600 and 1000 m; Weetman and Prescott 2000). Similar to other studies, we found that western hemlock trees, seedlings, and saplings can remain suppressed for decades in the understory until small gap-forming disturbances create space in the canopy (Kobe and Coates 1997). Dense patches of Sitka spruce seedlings were found on nurse logs within the zonal forest type but were rarely observed in other age classes (Appendix S1: Fig. S4). This is a strong contrast to the perhumid rainforests of Southeast Alaska where Sitka spruce is a co-dominant species across a range of site types (Alaback 1982). Unfortunately, our sampling approach could not fully capture the presence of Sitka spruce and western hemlock seedlings regenerating on nurse logs that were suspended sometimes greater than a meter above the forest floor in the zonal forest vegetation type.

Records of synchronous and sustained periods of radial growth in previously suppressed trees reveal that fine-scale disturbances—for example, occurring on average every 52 yr in beech forests of New Zealand—create small openings which support the growth of understory trees (Stewart et al. 1991). We found that the recruitment of canopy-dominant species in the study area was relatively constant over the last 300 yr, with the number of growth releases and recruitment pulses varying between zonal (every 34 yr) and bog forest (every 69 yr) vegetation types (Fig. 3; Appendix S2: Table S2). Patterns of relatively frequent releases also support the idea that individual trees may require multiple release/suppression events prior to reaching the canopy (Lertzman 1989). Our analyses also revealed that fine-scale disturbances—and/or favorable conditions in edaphic gaps (Lertzman et al. 1996)—allow shade-intolerant species such as shore pine to establish and grow in the zonal forest and bog forest vegetation types (Fig. 6). Although evidence of growth releases in multiple species and sites suggests the presence of continuous recruitment, we did not selectively sample canopy gaps as a result of recently felled trees to ground truth and validate more contemporary growth release events (Gutiérrez et al. 2008).

Western redcedar trees are often the largest (widest dbh and tallest, along with Sitka spruce) and the oldest trees within a stand (along with yellow-cedar), routinely reaching more than 1000 yr old (Appendix S2: Table S3). This is likely due to a combination of factors such as a long residence time within the canopy, ability to regenerate quickly in gap openings, and tolerate long periods of growth suppression in the understory (Daniels 2003). Additionally, the long lifespan of western redcedar and yellow-cedar trees increases their chances of survival in the understory until a canopy gap forms. Irregular bouts of yellow-cedar, and likely western redcedar, recruitment every few hundred years may be important for maintaining these species in the community (Lertzman 1995). Our results show that western redcedar and yellow-cedar are also long-lived dominants in the comparatively open conditions of bog woodlands which generally contain trees that are smaller in height and diameter due to edaphic conditions that limit tree growth rates (Kranabetter et al. 2003). Interestingly, western redcedar and yellow-cedar were found to dominate only the upper canopy layers in the zonal

forest and bog forest vegetation types. Although the bog woodland and blanket bog vegetation types have abundant light as a result of few and small overstory trees, these vegetation types are nutrient-limited, and the blanket bog vegetation type is dominated by shore pine which tolerates very wet, nutrient-poor, and acidic soil conditions (Fig. 3). Shore pine growing in blanket bogs are predominantly less than 7.5 cm dbh, less than 10 m height, and less than 200 yr in age (Figs. 3, 4; Burns and Honkala 1990).

We found that vegetation type was not a strong predictor of tree age in the study area and the oldest trees (~1000 yr) tend to be shorter in stature, smaller in circumference, and predominantly located in upland bog forest and bog woodland vegetation types (Fig. 2). This pattern is mostly in contrast to old-growth forest structure in other areas of coastal and inland BC, where old trees are primarily found in low densities and are the largest (tallest and widest) in the stand (Parish et al. 1999, Parish and Antos 2004). It is important to note that this pattern is not evident in the blanket bog vegetation type, which is characterized by shallow and acidic soils, younger trees, lower conifer diversity, and significantly lower stem density when compared to the three other vegetation types (Fig. 4).

Conclusions

Our research provides important contributions to understanding stand structure and dynamics in extensive and understudied hypermaritime forests in the Pacific temperate rainforest region. Our dendrochronological record extending 1350 yr, offers a rare examination of forest change through time and the role of small-scale disturbances in shaping old-growth forest structure and composition. Coastal temperate rainforests dominated by western redcedar have greatly influenced concepts and policies concerning old-growth forest conservation in BC, yet their old-growth structure, dynamics, and general ecology are not well understood across the broad spatial and growth gradients of the coast (Mackinnon 2003, Wong et al. 2003). Tall and productive old-growth forests of coastal BC have unique structure and function (Lertzman et al. 1996, Frazer et al. 2000, Giesbrecht et al. 2017) and have been greatly reduced through

both clear-cut and selective logging (Pearson 2010, Shackelford et al. 2018). The shorter and less productive old growth of the hypermaritime rainforest is well represented in protected areas (Price et al. 2020), yet remains understudied in terms of stand structure and dynamics. Despite low timber values, these old-growth hypermaritime forests contain large soil carbon stores (McNicol et al. 2019) and distinct biodiversity (Heger et al. 2018). Our research indicates that a combination of fine-scale disturbances and edaphic constraints promote ecologically complex patterns and processes in these forests (Trant et al. 2016, Hoffman et al. 2018).

Acknowledgments

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