LUND UNIVERSITY

Postglacial evolution and spatial differentiation of seasonal temperate rainforest in western Canada

Brown, K. J.; Nielsen, Anne Birgitte; Fitton, R. J.; Hebda, R. J.

Published in:
The Holocene

DOI:
10.1177/0959683608091783

2008

Citation for published version (APA):
Brown, K. J., Nielsen, A. B., Fitton, R. J., & Hebda, R. J. (2008). Postglacial evolution and spatial differentiation of seasonal temperate rainforest in western Canada. *The Holocene*, *18*(5), 715-727. https://doi.org/10.1177/0959683608091783

Total number of authors:
4

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

Post-glacial evolution and spatial differentiation of seasonal temperate rainforest in western Canada

Brown, K.J.[1,2,*], Nielsen, A.B.[2], Fitton, R.J.[1], Hebda, R.J.[1,3,4,5]

Royal British Columbia Museum[1], 675 Belleville St., Victoria, British Columbia, Canada, V8W 9W2; Department of Quaternary Geology[2], Geological Survey of Denmark and Greenland, Øster Voldgade 10, DK-1350 Copenhagen, Denmark; [3]Department of Biology and Schools of [4]Earth and Ocean Sciences and [5]Environmental Studies, University of Victoria, Victoria, Canada V8W 2Y2

*Corresponding Author:

Kendrick Brown
Department of Quaternary Geology
Geological Survey of Denmark and Greenland
Øster Voldgade 10
DK-1350 Copenhagen
Denmark

Telephone: +45 38 14 23 61
Facsimile: +45 38 14 20 50
Email: kbr@geus.dk

Abstract

Surface samples from Vancouver Island, Canada, were used to assess the relationship between discrete seasonal temperate rainforest (STR) plant communities and their corresponding pollen signatures. Pollen from 10 sediment cores was further used to evaluate the post-glacial development of these communities. Principal components analysis (PCA) of the surface data revealed the distinctiveness of the modern pollen rain, with samples from the Coastal Douglas Fir (CDF) zone, the dry Coastal Western Hemlock (CWH) zone, the wet CWH sub-zones and the Mountain Hemlock (MH) zone clustering distinctly. PCA of the fossil data revealed early-seral open canopy, wet rainforest, subalpine rainforest and late-glacial plant associations and showed that the STR has changed markedly through time. *Pinus* woodlands with low palynological richness prevailed in the early late-glacial period, only to be supplanted by mixed conifer forest with increased pollen richness. In the early Holocene, STR vegetation differentiated spatially as early-seral open canopy forests expanded, though a non-analog *Picea*-dominated forest persisted on the moist outer coast. Generally high pollen richness is attributed to the expansion of dryland habitat coupled with the development of a fire-maintained vegetation mosaic. In the mid and late Holocene intervals, open canopy communities persisted in eastern areas, eventually developing into modern CDF and dry CWH forest. In contrast, moist and oceanic CWH rainforest developed on central and western Vancouver Island, whereas subalpine forest established at high elevation. Pollen richness declined in the mid Holocene concomitant with increased precipitation and a general reduction in the incidence of fire, though this trend was offset somewhat in the late Holocene by paludification.

Keywords: rainforest, surface samples, pollen, vegetation, Holocene, British Columbia

1. Introduction

The seasonal temperate rainforest (STR) complex of western Canada is characterized by highly productive and diverse forests (Franklin and Dryness, 1973; Schoonmaker *et al.*, 1997) that contain some of the largest and oldest trees in the world (Waring and Franklin, 1979). Distinctive vegetation communities occur throughout the STR, with moist stands persisting in the outer oceanic region and dry stands occupying drier inland sites (Meidinger and Pojar, 1991). Cold-tolerant communities are found at high elevation where deep winter snow-packs blanket the landscape. The principal factors controlling the distribution of vegetation are the steep climatic gradients (precipitation and temperature) in the region (Peterson *et al.*, 1997; Brown *et al.*, 2006). Non-climatic factors that also regulate the distribution and configuration of the vegetation include landscape physiography, soil type and disturbance regime.

Pollen surface sample studies show that different forest communities located adjacent to one another can produce characteristic pollen signatures, illustrating that a spatially explicit sampling approach for paleoecological investigation is feasible in mountainous terrain with steep climatic gradients (Hebda and Allen, 1993; Allen *et al.*, 1999; Gavin *et al.*, 2001; 2005). Correspondingly, paleoecological investigations (Heusser, 1960; Mathewes, 1973; Heusser, 1983; Hebda 1983; 1995; Allen, 1995; Brown, 2000; Brown and Hebda, 2002a; Lacourse, 2005) have described the post-glacial vegetation and climate history of the STR. A predominately non-arboreal ecosystem existed sometime prior to the pine-dominated woodlands of the early late-glacial period (>14,000 calendar years before present [cal BP]) (Brown and Hebda, 2003), though the character, duration and extent of this community is poorly construed. Thereafter, it is widely accepted that pine expanded to dominate the landscape. In the late late-glacial interval (>11,400 cal BP), the pine woodlands yielded to widespread mixed conifer forest of hemlock, fir, and spruce under a cool moist climate. In the early Holocene interval (ca. 11,400-7,500 cal BP), xeric communities expanded in dryland regions under warm conditions, whereas spruce-hemlock forests persisted in the outer moist coastal zone. Modern rainforests gradually developed during the mid and late Holocene intervals (ca. 7,500-5000 and 5,000-0 cal BP respectively) as climate in the region gradually became wetter and cooler. At this time, both hemlock and cedar generally expanded in range and abundance throughout the region. Such regional reconstructions suggest that the temporal configuration of the rainforest was somewhat homogenous, with sites in similar physiographic settings often exhibiting comparable histories.

Here we seek to explore the link between modern vegetation communities and pollen assemblages from southern and central Vancouver Island where mountainous terrain and steep climate gradients prevail. If it can be shown that pollen assemblages correspond closely to modern plant communities, this relationship will be exploited to assess the post-glacial history of the STR. Particular emphasis will be placed on characterizing rainforest differentiation and ascertaining temporal measures of dissimilarity. Trends in post-glacial pollen richness will also be examined in order to compare the temporal patterns in floristic diversity between sites. In so doing, it will be possible to gain greater insight into the spatio-temporal evolution, variability and diversity of the coastal temperate rainforest complex of western Canada.

2. Study Area and Sites

Vancouver Island is the largest island in the eastern Pacific Ocean. It is located in the middle of the coastal temperate rainforest complex of western North America and demarcates the northern extent of the STR (Fig. 1). The landscape on Vancouver Island is highly diverse, with interior mountains yielding to hills and undulating coastal lowlands (Yorath and Nasmith, 1995). Precipitation decreases west to east and temperature varies with elevation. Cool moist winters and warm summers typify low-lying regions, whereas long cold winters with abundant snowfall and short cool summers characterize high elevations.

In British Columbia, Canada, plant communities are classified into zones according to the Biogeoclimatic Ecological Classification (BEC) of Meidinger and Pojar (1991). On Vancouver Island, 3 BEC zones dominate the STR complex, including the Coastal Douglas Fir (CDF) zone, Coastal Western Hemlock (CWH) zone and Mountain Hemlock (MH) zone. The CWH zone is further divided into four sub-zones (CWHxm, CWHmm, CWHvm, CWHvh) according to precipitation (xeric, moist, and very wet) and the degree of continentality (maritime to hypermaritime). Botanical nomenclature follows that of Douglas *et al.* (1994) and Hitchcock and Cronquist (1991).

The CDF zone is restricted to elevations below 150 m above sea level (asl) and occurs only on eastern Vancouver Island (Fig. 1). This zone is characterised by warm, dry summers and wet, mild winters. Typical trees include *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), *Thuja plicata* Donn. (western red cedar), *Abies grandis* (Dougl.) Lindl. (grand fir), *Arbutus menziesii* Prush. (arbutus), and *Alnus rubra* Bong. (red alder). Distinctive *Quercus garryana* Dougl. (Garry oak) and grassland communities are present in the driest portions of the CDF zone.

The CWH zone is juxtaposed to the west of the CDF and occurs at low to middle elevations (0-1,000 m asl). *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *T. plicata* predominate. *P. menziesii* occurs in dry parts of the zone, whereas *Abies amabilis* (Dougl.) Forbes (amabilis fir) and *Chamaecyparis nootkatensis* (D.Don) Spach (yellow-cedar) occupy wet portions. *Pinus contorta* Dougl. (lodgepole pine), *A. rubra*, *Picea sitchensis* (Bong.) Carr. (Sitka spruce) also occur within the CWH.

The Mountain Hemlock subalpine zone (MH) is restricted to elevations above 900 m asl. The most common trees associated with the MH include *Tsuga mertensiana* (Bong.) Carr. (mountain hemlock), *A. amabilis*, and *C. nootkatensis*. Other trees associated with the MH zone include *T. heterophylla*, *T. plicata*, and *Pinus monticola* Dougl. (western white pine).

A total of 142 surface samples were collected from 83 sites across central and southern Vancouver Island (Table 1; Fig. 1). In addition, 10 sediment cores were collected as part of this investigation: two from the CDF zone (Enos and Langford lakes), six from the CWH zone (East Sooke Fen (ESF), Boomerang, Turtle, Pixie, and Whyac lakes) and three from the MH zone (Harris Lake Ridge bog (HLRB), Porphyry and Walker lakes).

3. Methods

The collection and preparation of surface samples followed standard techniques (Allen *et al.*, 1999). The 10 sediment cores were collected using a modified Livingstone corer. The cores were sub-sampled for pollen analysis at a resolution between 2-20 cm depending on the length of record recovered and the degree of sediment homogeneity.

Pollen preparation followed standard techniques (Moore *et al.*, 1991). The cores were radiocarbon dated and the dates were calibrated to calendar years before present (cal BP) using CALIB 4.0 (Stuiver and Reimer, 1993). For each core, the calendar dates were plotted against depth and a curve was fit to the data using the Stineman function in the plotting program Kaleidagraph (Synergy Software, Reading, PA) to generate a locally-weighted (10% of data) least-squares smoothed age-depth model. The age-depth models were used to determine the age of each core sub-sample. Additional information regarding the basins, core stratigraphies and the number and sampling depths of the radiocarbon dates are reported in Brown and Hebda (2003), Fitton (2003) and Brown *et al.* (2006).

Principal component analysis (PCA) of the surface sample pollen data was used to assess the association between the vegetation in the BEC zones/sub-zones and its corresponding pollen signature. PCA was also performed on the fossil pollen data from each coring site to examine the temporal trends in vegetation development at each site. An advantage of using PCA to examine fossil pollen data from many sites is that it can yield insight into spatio-temporal correlations among pollen types. The length of the vectors in the PCA plots reveals the relative importance of each taxon, whereas the direction of the vectors reveals correlation. Vectors trending in the same direction imply a positive correlation, vectors trending in opposite directions imply a negative correlation and perpendicular vectors reveal no correlation between the taxa. PCA can also be used to elucidate vegetation history since the fossil data are stratigraphically arranged and may be plotted within the plant taxa loadings, thus revealing time transgressive associations at each site. Major deviations among sites can be attributed to regional vegetation response to primary forcing mechanisms such as climate change whereas subtle variations between neighboring sites likely reflect the local differences in biotic responses to climate change (Gavin *et al.*, 2001), disturbance, or human activity (Hebda and Mathewes, 1984; Brown and Hebda, 2002b).

Another PCA approach that can be used to assess the history of the STR is to plot the fossil pollen data within the PCA plot of the modern pollen spectra, thus revealing site evolution relative to modern vegetation (Odgaard and Rasmussen, 2000). This method also facilitates direct comparison between sites as the data for all cores are plotted in the same coordinate system. To achieve this, 3-point running average fossil pollen data from each core were included as passive samples in the PCA of the surface samples and plotted in the plane defined by the first two PCA axes of the surface samples. The running average was used to smooth the data in order to emphasize the dominant temporal trends. We limited this analysis to the Holocene since it is during this period that all trees that are currently dominant in the STR are present on Vancouver Island. For example, *P. menziezii* expanded on Vancouver Island only at the start of the Holocene (Hebda, 1995).

All PCA were conducted using CANOCO v. 4.5 (ter Braak and Smilauer, 2002). PCA was selected as the preferred ordination method because initial detrended correspondence analysis of the data showed that the gradient length of the first ordination axis in standard deviation units of species turnover was smaller than 2.0, indicating that a linear method was most appropriate (ter Braak and Smilauer, 2002). All taxa except aquatics were included in the PCA analyses and the data were centered by both sample and species and square-root transformed, as recommended for percentage data (ter Braak and Smilauer, 2002).

To obtain a measure of dissimilarity between modern and fossil samples, and in order to identify the closest modern analogues (Overpeck *et al*, 1985), the squared chord distance (SCD) from each fossil sample relative to each modern surface sample was calculated (Hammer and Harper, 2006). Dissimilarity indices such as SCD provide a measure of the degree of analogy between a fossil pollen assemblage and a modern surface sample (with low numbers representing greater similarity) and can be interpreted in terms of the resemblance of a past ecosystem to a modern ecosystem (Overpeck *et al.*, 1985). To facilitate the dissimilarity analysis, the surface samples were grouped into three categories (dry, wet, and high elevation). The dry category contained samples from the CDF zone and the CWHxm sub-zone whereas the wet category contained samples from the CWHmm-CWHvm/vh sub-zones. The high elevation category consisted of samples from the MH zone. These categories were designed so that each contained a sufficient number of modern pollen samples, thus permitting meaningful analysis. For each fossil sample, the mean SCD of the five closest analogues in each group was calculated and these values were used to assess the similarity between past and modern vegetation.

Dissimilarity can also be used to reveal intervals of non-analogous vegetation relative to the modern sample set. In this regard, the SCD to the closest analogue among all surface samples was recorded for each fossil sample. However, since there is no a-priori way of knowing the best threshold for separating analogous and non-analogous samples in a dataset, the threshold should be estimated by analyzing the distribution of dissimilarity among surface samples (Gavin et al, 2003). Therefore, the SCD between all pairs of surface samples were calculated and the distribution of SCD between samples within vegetation zones (analogues) and between vegetation zones (non-analogues) were determined (Fig. 2a). Because there was a relatively large overlap between the two distributions, the dissimilarity analysis is only partially effective at discriminating between analogous and non-analogous cases in this study (Gavin *et al.*, 2003), varying according to the threshold selected. The sensitivity of the analysis (the proportion of true analogues identified, TPF) increases with increasing threshold (Fig. 2b), whereas the specificity (the proportion of true non-analogues identified, TNF) decreases. The optimal decision threshold, with equal weight on maximizing sensitivity and specificity, can be found by maximizing the index TPF+TNF-1 as defined by Gavin *et al.* (2003). In this study, the index has a maximum value at SCD = 1.0 (Fig. 2b). Thus, fossil samples with SCD >1.0 to the closest modern sample were considered as not having a modern analogue. However, because of the large overlap between the SCD distributions of analogue and non-analogue samples, there is a 44% change that a sample identified as non-analogue actually does have an analogue.

Finally, the pollen richness of each fossil sample was calculated using rarefaction to a constant pollen sum of 240 grains which was the minimal number counted in any of the samples, thus correcting for the different pollen sums in each sample (Birks and Line, 1992). Rarefaction analysis is appropriate for use with pollen percentage data because it is less affected by differences in pollen representation between taxa compared to other measures of species diversity (Birks and Line, 1992). Rarefaction estimates are also sensitive to the presence of rare taxa, rendering the approach suitable for application with fossil pollen data. However, it is important to note that rarefaction is not a direct measure of floristic diversity, largely due to restrictions associated with taxonomic resolution, vegetation structure and differential pollen production and dispersal (Odgaard, 1999). Changes in the rarefaction estimate (hereafter referred to as pollen richness) of the number of pollen types through time, may, however, be related to changes in both vegetation diversity and degree of disturbance (Odgaard, 2001).

4. Results

4.1. Modern Pollen-Vegetation Signals

The first and second PCA axes of the modern pollen and spore spectra account for 40.3% of the variation in the data from Vancouver Island (Table 2, Fig. 3). This PCA reveals that the BEC zones generally produce characteristic pollen assemblages.

Rain-shadow regions of east Vancouver Island support grasslands and oak woodland and their respective spectra clustered distinctly in the ordination. The main difference is that the grassland samples are influenced by Poaceae pollen and *Pteridium* spores, whereas the woodland samples are characterized by *Q. garryana* and Poaceae pollen, as would be expected in an oak savanna with associated meadows.

Dry CDF rainforest has relatively high scores on the first and second PCA axes and is characterized by high proportions of *P. menziesii*, Poaceae and *Pteridum* and low occurrences of *T. heterophylla* and *T. mertensiana*. The dry CWH rainforest (CWHxm) is also generally discernable, with samples clustering close to the origin of the ordination plot. Such a distribution suggests that this community contains intermediate amounts of the dominant pollen taxa that are found throughout the STR complex. Allen *et al.* (1999)

corroborate this interpretation by showing that the CWHxm contains arboreal pollen types that also typify other BEC zones and sub-zones. The CWHxm probably contains a regional pollen mixture because it occurs in the transitional between the wet CWH and dry CDF communities and is located near the MH zone.

In contrast to the dry STR communities, samples from the moist CWHmm sub-zone have variable PCA scores (especially on axis 2) and are not readily distinguishable from the wet CWHvm/vh sub-zones or from the MH zone. The lack of clustering between CWHmm samples likely reflects the large variation in composition within that sub-zone, with moist climax stands being heavily influenced by *Abies* compared to early-seral or riparian sites that contain abundant *Alnus*. Tight clustering recurs with CWHvm/vh samples as evidenced by relatively low scores on the second PCA axis. These samples exhibit notable influence from *Picea*, *Alnus* and ferns. Samples from the MH zone also cluster, with consistently low scores on the first PCA axis and high scores on the second. MH zone samples are characterized by high abundances of *T. mertensiana*, *Abies* and *T. heterophylla* pollen. However, the *T. heterophylla* signal is likely due the to upslope transport of pollen from CWH forest at slightly lower elevation and not indicative of the local presence of this species in the MH zone.

4.2. Vegetation Associations

The PCA of the fossil pollen data showed that the first and second PCA axes explained 64.5-80.7% (Table 2) of the variance in the data. On Vancouver Island, several associations in the form of recurrent groups of correlated taxa emerge from the PCA (Fig. 4). One such association that includes *P. menziesii* and *Alnus* and sometimes *Pteridium* and Rosaceae (rose family) is evident at Enos, Langford, Boomerang, Pixie, Porphyry and Walker lakes, predominately in the early Holocene interval. Another generally recognizable association includes *T. heterophylla* and Cupressaceae (cedar-cypress family) pollen. *T. mertensiana* and *Abies* coupled with *Picea* and Cyperaceae are associated at some sites including Enos, Boomerang, Turtle, Pixie and to a lesser degree Langford and Walker lakes. A final association evident at Enos, Turtle, Whyac, Walker and Porphyry lakes as well as ESF involves *Pinus* and *Artemisia*.

4.3. Rainforest Development and Differentiation

The onset of each paleoecological record is marked by notable influence from *P. contorta* pollen (Fig. 4), likely produced by the expansive pine woodlands of the early late-glacial interval (>14,000 cal BP; Hebda and Whitlock, 1997). Thereafter, the association of *Picea* with *T. mertensiana* and *Abies* characterizes the late late-glacial interval (>11,400 cal BP). In the early Holocene (ca. 11,400-7500 cal BP), many of the sites from eastern and central Vancouver Island (Enos, Langford, Boomerang, Turtle and Pixie lakes as well as ESF) record associations of *P. menziesii*, *Alnus* and *Pteridium*. Even at high elevations, sites such as Porphyry and Walker lakes also appear influenced by the *P. menziesii*, *Alnus* and *Pteridium* association at this time. The pollen signature from HLRB is more ambiguous compared to Porphyry and Walker lakes, but it clearly shows a trend away from *Alnus* and *Pteridium* influence towards *Tsuga*. On western Vancouver Island at Whyac Lake, the early Holocene interval is not associated with early-seral indicators but rather with *Picea* and *T. heterophylla*. Through time, the trend towards *T. heterophylla* and away from *Picea* implies that hemlock gradually replaced spruce as the forest dominant.

The mid Holocene interval (ca. 7500-5000 cal BP) appears to be a period of transition for many sites on Vancouver Island. During this interval, the vegetation on eastern and central Vancouver Island trends away from the early-seral association previously mentioned and towards a modern rainforest configuration. On western Vancouver Island, this interval is marked by increasing influence by Cupressaceae (likely *T. plicata*) as well as non-arboreal types such as Cyperaceae. Transition is also noted at high elevation where early-seral associations gradually yield to climax vegetation of *T. heterophylla*, Cupressaceae (likely *C. nootkatensis*) and *T. mertensiana*.

The late Holocene interval (ca. 5000-0 cal BP) is characterized by the establishment of modern vegetation communities. *T. heterophylla*, Cupressaceae (*T. plicata*) and *Q. garryana* as well as *Abies* and *P. menziesii* exhibit notable influence at Enos and Langford lakes, marking the development of dry CDF forest on eastern Vancouver Island. Development of CWHxm rainforest is also apparent in the late Holocene at ESF and Boomerang Lake as *T. heterophllya*, Cupressaceae (*T. plicata*) and *Pteridium* exercise considerable influence. At Turtle Lake, CWH rainforest development is characterized by *T. heterophllya*, Cupressaceae (*T. plicata*) and *Myrica* (sweet gale). At Pixie and Whyac lakes, *T. heterophylla* and Cupressaceae (*T. plicata*) are highly influential, congruous with the development of wet western hemlock-dominated rainforest. The MH sub-alpine community is established at high elevation during the late Holocene.

4.4. Past to Present Rainforest Comparisons

When plotted in the PCA of the modern surface samples (Fig 5), the Holocene pollen assemblages from eastern Vancouver Island (Enos, Langford, Boomerang and Turtle lakes as well as ESF) plot consistently among the dry CDF and CWHxm surface samples, implying that dry-character rainforest has persisted on eastern Vancouver Island for the Holocene. In contrast, the vegetation on central Vancouver Island (Pixie and Whyac lakes) and at high elevation (Porphyry and Walker lakes as well as HLRB) has experienced more marked change as dry rainforest yielded to moist and sub-alpine rainforest respectively during the early to mid Holocene transition.

While this approach is useful in capturing the general essence of Holocene vegetation change relative to modern, it also rendered a few discrepancies compared to the history of vegetation change that was documented using the fossil pollen sample scores plotted within the species loadings (Fig. 4). One such discrepancy is the apparent shift from dry to wet rainforest at Whyac Lake during the early to mid Holocene transition (Fig. 5), even though it was previously shown that wet *Picea*-dominated rainforest yielded to wet *Tsuga*-dominated rainforest at this time (Fig. 4). This discrepancy may be an artifact of the method since early and mid Holocene fossil samples from Whyac Lake are forced to plot within the surface sample ordination even though they display high dissimilarity to the modern samples, and in one case even lack a modern analogue (Fig. 6). The *Picea*-dominated fossil samples plot within the modern CWHxm surface spectra possibly because of the presence of a few *P. menziesii* pollen grains in that part of the record, giving an erroneous impression of a dry to wet rainforest transformation.

Another discrepancy is found in the late Holocene at Porphyry and Walker lakes (Fig. 5). In this part of the record, the fossil samples do not trend into the MH surface samples even though both of these sites are currently surrounded by *T. mertensiana*-dominated forest. This observation is surprising given that the modern MH surface samples are clearly distinguishable from the other surface samples (Fig. 3) and that *T. mertensiana* is abundant in the late Holocene at Porphyry and Walker lakes (Fig. 4). Perhaps this discrepancy is related to the upslope transport of *T. heterophylla* pollen into the lakes in the MH zone.

4.5. Dissimilarity and Non-Analogy

The dissimilarity analysis reveals that the late-glacial basal sections in many of the cores exhibit a high degree of dissimilarity to modern samples (Fig. 6). In the Holocene, many of the dry sites exhibit minimal dissimilarity with modern dry CDF and CWHxm rainforest. For example, low dissimilarity is noted at Enos Lake from ca. 8000-4000 cal BP, at Langford Lake from ca. 10,500 cal BP-present, at ESF from ca. 10,500-1,500 cal BP and at Boomerang Lake from ca. 10,000-2,000 cal BP. On central Vancouver Island, Pixie Lake shows minimal dissimilarity with dry rainforest for only a short period from ca. 11,500-10,000 cal BP, thereafter exhibiting small dissimilarity with wet rainforest for the remainder of the Holocene. In comparison, no clear patterns are evident at Turtle Lake. On the wet western coast, Whyac Lake consistently exhibits high dissimilarity to the modern samples, though the smallest values appear to correspond with wet rainforest. Further, the optimal threshold method reveals that one early

Holocene sample from Whyac Lake has no analogue within the modern surface sample set.

At high elevation, Porphyry Lake appears least dissimilar to wet rainforest between ca. 11,500-4,000 cal BP. During the late Holocene, however, it exhibits small dissimilarity to both wet and high elevation forests. Similarly, Walker Lake is least dissimilar to wet rainforest in the early and mid Holocene from ca. 10,000-5,000 cal BP and thenceforth least dissimilar to high elevation rainforest. This trend is indicative of sub-alpine forest development that was not clear in the fossil-surface pollen PCA (Fig. 5). HLRB likewise records minimal dissimilarity to high elevation rainforest during the late Holocene. One late Holocene sample from HLRB is identified as having no modern analogue within the surface sample set.

4.6. Temporal Pollen Richness

Comparison of the pollen richness curves from lowland sites on Vancouver Island reveals generally low measures of pollen richness during the early late-glacial interval dominated by *Pinus* (Fig. 7). Pollen richness increased during the late late-glacial interval as mixed conifer forests expanded on Vancouver Island, with Whyac Lake being the only exception. The ambiguity at Whyac Lake is not surprising given the possibility of a repeating stratigraphic section at the bottom of that sediment core (Brown and Hebda, 2002a).

In the early Holocene interval, relatively high pollen richness is noted at all lowland sites on eastern Vancouver Island. On central Vancouver Island, Turtle Lake is characterized by an increase in pollen diversity similar to the more eastern sites, whereas at Pixie Lake the difference in pollen richness between the late-glacial and early Holocene is small, a surprising observation given that the incidence of fire disturbance at Pixie Lake in the early Holocene was markedly greater than during the late late-glacial interval (Brown and Hebda, 2002a). It is thought that the increase in the incidence of fire would have facilitated a greater vegetation mosaic and consequently higher pollen richness, though this trend was not observed. At Whyac Lake, the increase in pollen richness during the early Holocene is consistent with the increase noted from eastern sites. In the mid and late Holocene, a general reduction in pollen richness is noted on eastern and central Vancouver Island. The exceptions to this trend include ESF, the last 2000 years at Turtle Lake, and Whyac Lake.

At the high elevation sites, no marked changes in pollen richness are observed during the late-glacial period. In the early Holocene, a reduction in diversity is noted at Porphyry Lake whereas a slight increase is observed at HLRB that is consistent with lowland sites. No change in richness is evident at Walker Lake during the early Holocene. In the mid Holocene, opposite trends are again noted at Porphyry Lake and HLRB, with the former experiencing a slight increase in richness and the latter a decrease. Walker Lake remains unchanged. In the late Holocene, Porphyry and Walker lakes show no change in diversity from the mid Holocene, whereas an increase in pollen richness is noted at HLRB.

5. Discussion

In the topographically variable coastal landscape of western Canada, unique STR vegetation (BEC) zones (Meidinger and Pojar, 1991) are juxtaposed across steep climate gradients. On Vancouver Island, these zones generally produce diagnostic pollen signatures that are reflective of the vegetation (Fig. 3). Other investigations have likewise documented good correspondence between pollen assemblages and vegetation in regions characterized by steep environmental gradients and zoned vegetation (Dunwiddie, 1987; Hebda and Allen, 1993; Gavin *et al.*, 2005), revealing the applicability and usefulness of the modern surface spectra in paleoecological investigations from such settings. For example, the 40.3% variation explained by the first and second PCA axes of the modern pollen and spore spectra from Vancouver Island (Table 2, Fig. 3) is similar to that determined in a detrended correspondence analysis of modern samples in the Olympic Peninsula (42.8%, Gavin *et al*., 2005).

Given that plants respond individually to ecosystem forcing and disturbance (Davis, 1981; Hebda, 1998), identifiable plant associations in the form of recurrent groups of correlated taxa in the PCA (Fig. 4) may be representative of a vegetation response to a recurring ecosystem process such as fire disturbance, a temporal state of ecosystem stability (termed a biogeochron by Hebda and Whitlock, 1997) or spatially extensive vegetation. For example, the association of *P. menziesii*, *Alnus*, Rosaceae and *Pteridium* likely reflects either open or fire disturbance-adapted plant communities because the plants in this group are recognized as being shade intolerant, early-seral or fire adapted (Pojar and MacKinnon, 1994). Indeed, it has previously been shown that an increase in the incidence of fire in the early Holocene fostered an increase in early-seral *Alnus* and *Pteridium* in coastal British Columbia, Canada (Mathewes, 1973; Brown and Hebda, 2002a), consistent with the association identified in the PCA. In contrast, the association of *T. heterophylla* and Cupressaceae pollen likely reflects the long-term persistence of these taxa in moist areas characterized by closed canopies and little fire disturbance. *T. mertensiana* and *Abies* coupled with *Picea* and Cyperaceae are associated because they were important components of the late late-glacial vegetation ca. 14,000-11,400 years ago and currently characterize the MH zone. Likewise, *Pinus* and *Artemisia* are associated because they were important constituents of the early late-glacial vegetation on Vancouver Island >14,000 cal BP (Hebda, 1995). The identification and recognition of such associations is useful because they can help discern the historic configuration of the STR.

Previous paleoenvironmental investigations have revealed that the STR complex of western Canada has a legacy of transformation that extends at least to the end of the last ice age (eg. Heusser, 1960; Hebda, 1995; Alley and Chatwin, 1979). Several studies document the existence of a herb-shrub dominated community in coastal British Columbia that preceded the *Pinus* woodlands of the early late-glacial interval (>14,000 cal BP). It is postulated that this assemblage existed as either a full-glacial coastal refugium (Mathewes, 1989; Brown and Hebda, 2003) or as a pioneering community (Brown and Hebda, 2003; Lacourse, 2005). Of the sites analyzed in this investigation, only Porphyry Lake contains this non-arboreal assemblage (Brown and Hebda, 2003). The assemblage is not clearly visible in the PCA plot (Fig. 4) because *Pinus* pollen overwhelmed the typically underrepresented non-arboreal contribution (Hebda and Allen, 1993; Allen *et al.*, 1999). However, dissimilarity analysis reveals that the non-arboreal assemblage at Porphyry Lake is clearly dissimilar to vegetation in the modern STR.

In the early late-glacial interval, *Pinus* woodlands expanded regionally in the coastal zone (Hebda, 1995), even colonizing previously exposed continental shelf

(Lacourse *et al.*, 2003). Given the association between *Pinus* and *Artemisia*, it is likely that *Artemisia* occupied openings in the woodlands. These woodlands were highly dissimilar to any modern forest in the STR and were characterized by low pollen richness, which could be related to a number of factors including post-glacial migration or colonization lags (Pertraitis *et al.*, 1989) or to the prevailing cold dry climate (Hebda, 1995; Gaston, 2000).

Thereafter, the *Pinus* woodlands were replaced by mixed conifer forest as *Picea*, *T. mertensiana* and *Abies* expanded in the region during the late late-glacial interval (>11,400 cal BP). The occasional association in ordination space between these taxa and Cyperaceae suggests that wetlands occupied moist areas within the forest (Fig. 4). Even though the forest contained assorted conifers like the STR today, it exhibits little similarity to the modern STR complex, suggesting that species occurred in different relative abundances compared to present. It was, however, characterized by increased pollen richness compared to the preceding *Pinus* woodlands, likely related to factors such as species and wetland expansion combined with intermittent fire disturbance (Cwynar, 1987; Brown and Hebda, 2002a; 2003; Heinrichs *et al.*, 2002). While this forest type appears in many pollen diagrams from Vancouver Island (Hebda, 1983; Brown and Hebda 2002a; 2003; Fitton, 2003), implying that it was widespread and somewhat homogeneous, the particularly strong fern signal at HLRB reveals an element of spatial variability in forest composition and structure. Perhaps the fern signal at HLRB is associated with local open patches (Fitton, 2003).

In the early Holocene interval (11,400-7,500 cal BP), early-seral and open structure rainforest, palynologically similar to the modern CDF zone, expanded in the

STR region (Figs. 4 and 5). This rainforest persisted not only on eastern and central Vancouver Island, but also possibly at high elevation as evidenced by the influence of the *P. menziesii*, *Alnus* and *Pteridium* association (Fig. 4). It is important to note, however, that upslope pollen transport may have contributed some lowland pollen to the high elevation sites. This early-seral and open structure rainforest was palynologically diverse (Fig. 7), likely because of the expansion of dryland communities under warm dry climatic conditions coupled with the existence of a well developed vegetation mosaic maintained by a high incidence of fire disturbance (Cwynar, 1987; Brown and Hebda, 2002a). The strong rosaceous signal noted at Boomerang, Turtle and Walker lakes supports the concept of spatial variability in floral composition. While widespread, these dry forests did not occur in the outer coastal region. Instead, closed canopy *Picea*-dominated forest persisted in the moist coastal zone.

In contrast to the dry open canopy rainforest to the east, the *Picea*-dominated rainforest was dissimilar to the modern forests on Vancouver Island. One sample even exhibited non-analogy, highlighting the true uniqueness of that coastal rainforest. In addition to occupying the outer coast on southern Vancouver Island, the documentation of *Picea*-*T. heterophylla* forest on northern Vancouver Island ca. 350 km north (Hebda, 1983; Lacourse, 2005) implies that this forest type was an extensive coastal assemblage that persisted for several thousand years. Consistent with the early-seral and open structure rainforest to the east, the coastal *Picea*-dominated forest was characterized by increased pollen richness, perhaps related to occasional fire or wind disturbance (Brown and Hebda, 2002a). A recent spatio-temporal precipitation reconstruction (Brown *et al.*, 2006) reveals a spatial pattern in early Holocene precipitation that is consistent with the spatial distribution of vegetation noted here, implying that the development of the modern precipitation gradient in the early Holocene was likely a key regulatory factor that influenced vegetation distribution.

Further differentiation and changes in rainforest composition occurred during the mid and late Holocene intervals (7,500-5,000 and 5,000-0 cal BP respectively). Open canopy rainforest continued to persist in dry areas (Figs. 4 and 5), whereas closed canopy *T. heterophylla*-*T. plicata* dominated rainforest expanded in the moist and montane regions of Vancouver Island (Hebda, 1973; 1995; Mathewes, 1989; Whitlock, 1992). At high elevation, *T. mertensiana* and *C. nootkatensis* became increasingly important as modern sub-alpine communities developed (Brown and Hebda, 2003; Fitton, 2003). Coincident with these changes is a general decline in lowland pollen richness during the mid Holocene that is likely related to increased regional moisture (Brown *et al.*, 2006), a reduction in fire disturbance and the development of closed canopies. Renewed lowland pollen diversity, however, is noted in the late Holocene at some sites as wetlands developed throughout the STR complex in response to prolonged wet conditions (Hebda, 1983; 1995; Brown and Hebda, 2002a). For example, Cyperaceae is an important vegetation component at both ESF and Whyac Lake during the late Holocene, reflecting local wetland development concomitant with increased precipitation (Brown *et al.*, 2006). The preponderance of *Myrica* at Turtle Lake likely reflects the local presence of sweet gale around the shoreline, also indicating wetland development. In addition to the development of scattered wetlands, further evidence of increased floral richness and spatial variability is found at HLRB, where the notable influence of ericaceous pollen indicates local heathland development during the last millennia. In summary, the STR has differentiated profoundly during the Holocene in response to changes in temperature and precipitation. Ecological processes such as fire disturbance and wetland development have further contributed to the spatial variability of forest composition and diversity.

6. Conclusions

PCA of modern pollen spectra reveals that discrete vegetation zones on Vancouver Island produce a characteristic pollen rain, with exception of the CWHmm zone. Distinguishable communities include grassland and *Q. garryana* associations, the dry CDF zone, CWHxm and CWHvm/vh sub-zones and the MH zone. Further, species loadings from the PCA reveal several pollen associations, including an early-seral open canopy association, a closed canopy *T. heteropllya*-Cupressaceae (likely *T. plicata*) association, a high elevation *T. mertensiana-Abies* association, and late-glacial biogeochron associations of *Pinus-Artemisia* and possibly *T. mertensiana-Abies-Picea*.

The vegetation in the STR region has experienced remarkable transformation through time, ranging from non-arboreal vegetation at Porphyry Lake to widespread *Pinus* woodlands and mixed conifer forest in the late-glacial period. During the Holocene, the vegetation in the STR complex differentiated along climate gradients. In the early Holocene early-seral and open canopy forest occupied dry regions, whereas *Picea*-dominated forest persisted along the wet outer coast. Further differentiation during the mid and late Holocene ultimately culminated in modern STR communities. Throughout the Holocene, climate evolution coupled with ecological processes such as fire disturbance and wetland expansion influenced palynological richness. Consequently, these factors will likely be important regulators of future diversity as the STR complex responds to global climate forcing and change.

6. Acknowledgements

We wish to thank the Natural Sciences and Engineering Council of Canada (NSERC) for funding through grant no. OGP0090581 to R. Hebda. We also thank the University of Victoria for graduate student funding and Dave Gillan and Qibin Zhang for their contributions. We are also grateful to the two anonymous reviewers who provided thoughtful and constructive evaluation that improved the manuscript.

References

Allen, G.B. 1995: Vegetation and climate history of southeast Vancouver Island, British Columbia. M.Sc. Thesis. School of Earth and Ocean Sciences, University of Victoria, Victoria, British Columbia, Canada, pp.143.

Allen, G.B., Brown, K.J., and Hebda, R.J. 1999: Modern pollen spectra from south Vancouver Island. *Canadian Journal of Botany* 77, 1-14.

Alley, N.F. and Chatwin, S.C. 1979: Late Pleistocene history and geomorphology, southwestern Vancouver Island, British Columbia. *Canadian Journal of Earth Sciences*, 16: 1645-1657.

Birks, H.J.B. and Line, J.M. 1992: The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *Holocene* 2: 1-10.

Brown, K.J. 2000: Late-Quaternary vegetation, climate, fire history, and GIS mapping of Holocene climates on southern Vancouver Island, British Columbia, Canada. Ph.D. Dissertation. School of Earth and Ocean Sciences, University of Victoria, Victoria, British Columbia, Canada, pp. 253.

Brown, K.J. and Hebda, R.J. 2002a: Origin, development, and dynamics of coastal temperate conifer rainforests of southern Vancouver Island, Canada. *Canadian Journal of Forest Research* 32, 252-272.

Brown, K.J. and Hebda, R.J. 2002b: Ancient fires on Southern Vancouver Island, British Columbia, Canada: A change in causal mechanisms at about 2,000 ybp. *Environmental Archaeology* 7, 1-12.

Brown, K.J. and Hebda, R.J. 2003: Coastal rainforest connections disclosed through a Late Quaternary vegetation, climate, and fire history investigation from the Mountain hemlock zone on southern Vancouver Island, British Columbia, Canada. *Review of Palaeobotany and Palynology* 123, 247-269.

Brown, K.J., Fitton, R.J., Schoups, G., Allen, G.B., Wahl, K.A. and Hebda, R.J. 2006: Holocene precipitation in the coastal temperate rainforest complex of southern British Columbia, Canada. *Quaternary Science Reviews* 25, 2762-2779.

Cwynar, L.C. 1987: Fire and the forest history of the North Cascade Range. *Ecology* 68, 791-802.

Davis, M.B. 1981: Quaternary history and the stability of forest communities. In West, C.D., Shugart, H.H. and Botkin, D.B., editors, *Forest Succession: Concepts and Application*, Chapter 10, Springer-Verlag, New York.

Douglas, G.W., Straley, G.B. and Meidinger, D. 1994: The vasular plants of British Columbia. Special Report Series 1-4. Ministry of Forests.

Dunwiddie, P.W. 1987: Macrofossil and pollen representation of coniferous trees in modern sediments from Washington. *Ecology* 68, 1-11.

Fitton, R. J. 2003: Late Quaternary history of vegetation, climate and fire disturbance on south central Vancouver Island, British Columbia, Canada. M.Sc. Thesis. School of Earth and Ocean Sciences, University of Victoria, Victoria, British Columbia, Canada, pp.165.

Franklin, J.T. and Dyrness, C.T. 1973: Natural Vegetation of Oregon and Washington. U.S. Department of Agriculture Technical Report PNW-8, pp. 417.

Gaston, K.J. 2000: Global patterns in biodiversity. *Nature* 405, 220-227.

Gavin, D.G., McLachlan, J.S., Brubaker, L.B. and Young, K.A. 2001: Postglacial history of subalpine forests, Olympic Peninsula, Washington, USA. *Holocene* 11, 177-188.

Gavin, D.G., Oswald, W.W., Wahl, E.R. and Williams, J.W. 2003: A statistical approach to evaluating distance metrics and analog assignments for pollen records. *Quaternary Research* 60, 356-367.

Gavin, D.G., Brubaker, L.B., McLachlan, J.S. and Oswald, W.W. 2005: Correspondence of pollen assemblages with forest zones across steep environmental gradients, Olympic Peninsula, Washington, USA. *Holocene* 15, 648-662.

Hammer, Ø. and Harper, D. 2006: Paleontological Data Analysis. Blackwell Publishing. pp. 351.

Hebda, R.J. 1983: Late-glacial and post-glacial vegetation history at Bear Cove Bog, northeast Vancouver Island, British Columbia. *Canadian Journal of Botany* 61, 3172-3192.

Hebda, R.J. 1995: British Columbia vegetation and climate history with focus on 6 ka bp. *Géographie Physique et Quaternaire* 49, 55-79.

Hebda, R.J. 1998: Atmospheric change, forests and biodiversity. *Environmental Monitoring and Assessment* 49, 195- 212.

Hebda, R.J. and Allen, G.B. 1993: Modern pollen spectra from west central British Columbia. *Canadian Journal of Botany* 71, 1486-1495.

Hebda, R.J. and Mathewes, R.W. 1984: Holocene history of cedar and Native Indian cultures of the North American Pacific coast. *Science* 255, 711-713.

Hebda, R.J. and Whitlock, C. 1997. Environmental History. Chapter 9. In Schoonmaker, P.K., von Hagen, B. and Wolf, E.C., editors, *The Rainforests of Home*, Island Press, Washington D.C., 227-254.

Heinrichs, M.L., Antos, J.A., Hebda, R.J. and Allen, G.B. 2002: *Abies lasiocarpa* (Hook.) Nutt. in the late-glacial and early Holocene vegetation of British Columbia, Canada, and adjacent regions in Washington, U.S.A. *Review of Palaeobotany and Palynology* 120, 107-122.

Heusser, C.J. 1960: Late-Pleistocene environments of North Pacific North America. American Geographical Society special publication No. 35.

Heusser, L.E. 1983: Palynology and paleoecology of post-glacial sediments in an anoxic basin, Saanich Inlet, British Columbia. *Canadian Journal of Earth Sciences*, 20: 873-885.

Hitchcock, C.L. and Cronquist, A. 1991: Flora of the Pacific Northwest. University of Washington Press, Seattle and London.

Lacourse, T. 2005: Late Quaternary dynamics of forest vegetation on northern Vancouver Island, British Columbia, Canada. *Quaternary Science Reviews* 24, 105-121.

Lacourse, T., Mathewes, R.W. and Fedje, D.W. 2003: Paleoecology of late-glacial terrestrial deposits with in situ conifers from the submerged continental shelf of western Canada. *Quaternary Research* 60, 180-188.

Mathewes, R.W. 1973: A palynological study of post-glacial vegetation changes in the University Research Forest, southwestern British Columbia. *Canadian Journal of Botany*, 51, 2085-2103.

Mathewes, R.W. 1989: Paleobotany of the Queen Charlotte Islands. In Scudder, G.G.E. and Gessler, N., editors, *The outer shores*, Queen Charlotte Islands Museum Press, 75-90.

Meidinger, D. and Pojar, J. (Eds.). 1991: *Ecosystems of British Columbia*, Research Branch, Ministry of Forests, Province of British Columbia, Victoria, B.C., 81-124.

Moore, P.D., Webb, J.A. and Collinson, M.E. 1991: Pollen analysis: Second Edition. Blackwell Scientific Publications, Oxford, pp. 216.

Odgaard, B.V. 1999: Fossil pollen as a record of past biodiversity. *Journal of Biogeography* 26, 7-17.

Odgaard, B.V. 2001: Palaeoecological perspectives on pattern and process in plant biodiversity and distribution adjustments: a comment on recent developments. *Diversity and Distributions* 7, 197-201.

Odgaard, B.V. and Rasmussen, P. 2000: Origin and temporal development of macro-scale vegetation patterns in the cultural landscape of Denmark. *Journal of Ecology* 88, 733-748.

Overpeck, J.T., Webb, T. and Prentice, I.C. 1985: Quantitative Interpretation of Fossil Pollen Spectra: Dissimilarity Coefficients and the Method of Modern Analogs. *Quaternary Research* 23: 87-108.

Pertraitis, P.R., Latham, R.E. and Niesenbaum, R.A. 1989: The maintenance of species diversity by disturbance. *The Quaterly Review of Biology* 64, 393-418.

Peterson, D.L., Schreiner, E.G. and Buckingham, N.M. 1997: Gradients, vegetation and climate: spatial and temporal dynamics in the Olympic Mountains, U.S.A. *Global Ecology and Biogeography Letters* 6, 7-17.

Pojar, J. and MacKinnon, A. (Eds.). 1994: Plants of the Pacific Northwest Coast. Vancouver, BC: Lone Pine.

Schoonmaker, P.K., von Hagen, B. and Wolf, E.C. (Eds.). 1997: *The Rain Forests of Home: Profile of a North American Bioregion*, Island Press, Washington, D.C., USA.

Stuvier, M. and Reimer, P.J. 1993: Extended 14C database and revised CALIB radiocarbon calibration program. *Radiocarbon* 35, 215-230.

ter Braak, C.J.F. and Smilauer, P. 2002: CANOCO Reference Manual and CanoDraw for Windows User's Guide. Software for Canonical Community Ordination (version 4.5). Biometrics, Wageningen University, Wageningen.

Waring, R.H. and Franklin, J.F. 1979: Evergreen coniferous forests of the Pacific Northwest. *Science* 204, 1380-1386.

Whitlock, C. 1992: Vegetational and climatic history of the Pacific Northwest during the last 20,000 years: implications for understanding present-day biodiversity. *The Northwest Environmental Journal* 8, 5-28.

Yorath, C.J. and Nasmith, H.W. 1995: The geology of southern Vancouver Island: A field guide. Orca Book Publishers, Canada, pp. 8-15.

Table 1. Surface sample and sediment core site characteristics. BEC is the Biogeoclimatic Ecological Classification where CDFmm = Coast Douglas Fir moist maritime, CWHxm = Coastal Western Hemlock xeric maritime, CWHmm = Coastal Western Hemlock moist maritime, CWHvm = Coastal Western Hemlock very wet maritime, and CWHxh = Coastal Western Hemlock very wet hypermaritime.

Sample	Sample Type	Latitude (^{o}N)	Longitude (^{o}W)	Elevation (m)	BEC
S93-A-E	Surface litter	48.40	123.30	10	Grassland
S93-28-32	Surface litter	48.42	123.35	20	Garry oak
MT-1-6	Surface litter	48.45	123.32	97	CDFmm
BH-1-4	Surface litter	48.42	123.37	38	CDFmm
S94-3	Surface litter	48.48	123.44	90	CDFmm
S94-4	Surface litter	48.48	123.45	60	CDFmm
S94-1-2	Surface litter	48.49	123.45	85	CDFmm
RR-17-19	Surface litter	48.43	123.47	76	CDFmm
DL0-10	Surface lake	48.55	123.47	60	CDFmm
FL0-10	Surface lake	48.52	123.48	60	CDFmm
PL0-10	Surface lake	48.55	123.50	60	CDFmm
LL0-20	Surface lake	48.45	123.53	60	CDFmm
MB-1-6	Surface litter	48.45	123.60	410	CWHxm
S93-1	Surface litter	48.57	123.71	230	CWHxm
R8	Surface litter	48.65	123.73	280	CWHxm
S01-1-8	Surface litter	49.32	124.95	80	CWHxm
S01-4-5	Surface lake	49.32	124.95	80	CWHxm
S93-40	Surface litter	48.32	123.65	120	CWHxm
S93-36	Surface litter	48.34	123.68	100	CWHxm
S93-2-4	Surface litter	48.57	123.72	377	CWHxm
S93-5-7	Surface litter	48.57	123.73	633	CWHxm
S93-8	Surface litter	48.59	123.73	380	CWHxm
R7	Surface litter	48.66	123.74	400	CWHxm
S93-14	Surface litter	48.63	123.80	170	CWHxm
S93-9	Surface litter	48.87	123.84	800	CWHxm
MILE-11A-E	Surface litter	48.51	123.89	430	CWHmm
S95-8A	Surface litter	48.66	124.14	360	CWHmm
S95-9A	Surface litter	48.67	124.14	230	CWHmm
S95-7A	Surface litter	48.66	124.14	360	CWHmm
S95-6A	Surface litter	48.66	124.14	360	CWHmm
S95-5A	Surface litter	48.64	124.17	230	CWHmm
S95-3AE	Surface litter	48.61	124.19	180	CWHmm
SL-AE	Surface litter	48.59	123.86	530	CWHmm
MILE-21.5A-E	Surface litter	48.48	123.84	680	CWHmm
S93-12	Surface litter	48.90	123.87	1200	CWHmm
S83-16	Surface litter	48.68	123.92	1030	CWHmm
S93-25	Surface litter	48.69	123.93	1060	CWHmm
S02-35	Surface litter	49.03	124.33	1210	CWHmm
S02-36	Surface litter	49.03	124.33	1150	CWHmm
S01-18-19	Surface litter	49.22	124.62	920	CWHmm
S01-20-21	Surface litter	49.22	124.62	800	CWHmm
S01-17	Surface litter	49.23	124.62	1000	CWHmm
S95-4A	Surface litter	48.61	124.19	150	CWHvm

S91-6	Surface litter	48.60	124.23	40	CWHvm
S91-2	Surface litter	48.49	124.26	210	CWHvm
S95-1A-E	Surface litter	48.58	124.28	10	CWHvm
S91-5	Surface litter	48.59	124.29	20	CWHvm
S95-2A	Surface litter	48.59	124.33	10	CWHvm
S91-3-4	Surface litter	48.59	124.35	20	CWHvm
NL-4	Surface litter	48.83	124.70	40	CWHvm
NL-3	Surface litter	48.77	124.72	60	CWHvm
NL-2	Surface litter	48.77	124.72	80	CWHvm
NL-1	Surface litter	48.70	124.80	30	CWHvm
S83-54-56+58	Surface litter	48.48	124.11	697	CWHvm
S83-57	Surface litter	48.49	124.12	670	CWHvm
WL-1-4	Surface litter	48.67	124.84	10	CWHvh
WL-5	Surface litter	48.67	124.84	10	CWHvh
S91-10	Surface litter	48.81	125.12	50	CWHvh
S91-9	Surface litter	48.81	125.15	40	CWHvh
S83-50	Surface litter	48.79	125.16	10	CWHvh
S83-51-52	Surface litter	48.80	125.17	20	CWHvh
S02-34	Surface litter	49.05	124.37	1370	MHmm
S93-13	Surface litter	48.91	123.83	1120	MHmm
S93-10-11	Surface litter	48.90	123.84	1070	MHmm
S02-44-45	Surface litter	49.05	124.34	1290	MHmm
S02-32	Surface lake	49.05	124.34	1370	MHmm
S02-12	Surface litter	49.05	124.34	1383	MHmm
S02-15	Surface litter	49.05	124.34	1322	MHmm
S02-37	Surface litter	49.05	124.34	1160	MHmm
S02-51	Surface litter	49.06	124.35	1360	MHmm
S01-9-13	Surface litter	49.25	124.57	1220	MHmm
S01-14	Surface litter	49.25	124.57	1120	MHmm
S01-15	Surface litter	49.25	124.59	1100	MHmm
S02-19-20	Surface litter	49.06	124.34	1450	MHmm
S02-21-22	Surface litter	49.06	124.34	1460	MHmm
S02-28+30	Surface litter	49.06	124.34	1460	MHmm
S01-G-H	Surface litter	49.23	124.58	1514	MHmm
S01-I-J	Surface litter	49.23	124.58	1511	MHmm
S01-K	Surface litter	49.23	124.59	1422	MHmm
S01-C-D	Surface litter	49.23	124.60	1234	MHmm
S01-E-F	Surface litter	49.23	124.60	1340	MHmm
S01-A-B	Surface litter	49.23	124.60	1160	MHmm
S01-16	Surface litter	49.24	124.60	1080	MHmm
Enos	Sediment core	49.28	124.15	50	CDFmm
Langford	Sediment core	48.45	123.53	60	CDFmm
ESF	Sediment core	48.35	123.68	155	CWHxm
Boom	Sediment core	49.18	124.15	360	CWHxm
Turtle	Sediment core	49.32	124.95	80	CWHxm
Pixie	Sediment core	48.60	124.20	70	CWHvm
Whyac	Sediment core	48.67	124.84	10	CWHvh
Porphyry	Sediment core	48.91	123.84	1100	MHmm
Walker	Sediment core	48.53	124.00	950	MHmm
HLRB	Sediment core	49.73	125.24	1300	MHmm

Table 2. Cumulative percentage variance of species data explained by PCA axes.

Site	Axis 1	Axis 2	Axis 3	Axis 4
Boomerang	51.6	67.1	77.1	82.5
Enos	70.9	80.7	84.9	87.5
ESF	56.0	70.9	77.5	80.6
HLRB	47.8	68.3	77.2	84.1
Langford	51.3	64.5	73.9	78.9
Pixie	52.6	74.6	80.5	84.9
Porphyry	43.3	66.2	76.3	81.8
Turtle	53.9	65.3	74.5	79.7
Walker	48.7	74.1	80.1	83.6
Whyac	54.0	76.1	82.0	85.9
Surface	23.2	40.3	53.2	60.3

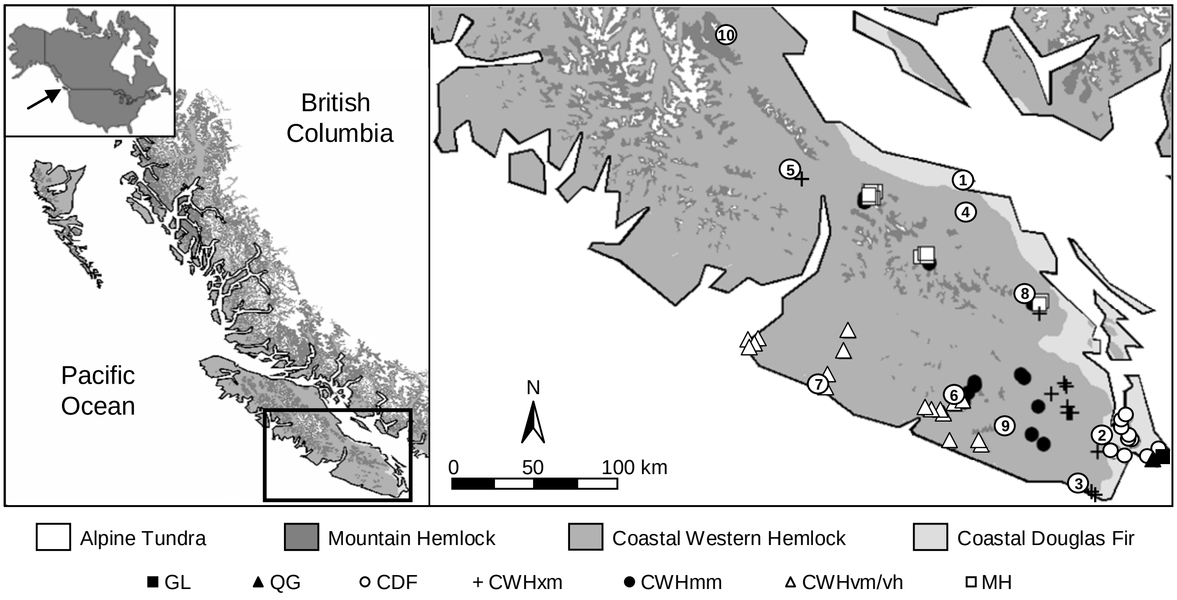

Figure 1. The left panel shows the continental location of the study site (inset arrow) as well as the distribution of the coastal temperate rainforest in British Columbia, Canada. The study site is located in the box. The right panel shows the locations of the surface samples (various symbols) and sediment cores (numbered circles as follows: 1. Enos Lake, 2. Langford Lake, 3. East Sooke Fen, 4. Boomerang Lake, 5. Turtle Lake, 6. Pixie Lake, 7. Whyac Lake, 8. Porphyry Lake, 9. Walker Lake and 10. Harris Ridge Lake Bog) on Vancouver Island. Shading represents the biogeoclimatic zones and the abbreviations are as follows: GL=grassland association, QG=Quercus garryana association, CDF=Coastal Douglas Fir zone, CWHxm=xeric maritime Coastal Western Hemlock sub-zone, CWHmm=moist maritime Coastal Western Hemlock sub-zone, CWHvm/vh=very wet maritime to hypermaritime Coastal Western Hemlock sub-zones, MH=Mountain Hemlock zone.

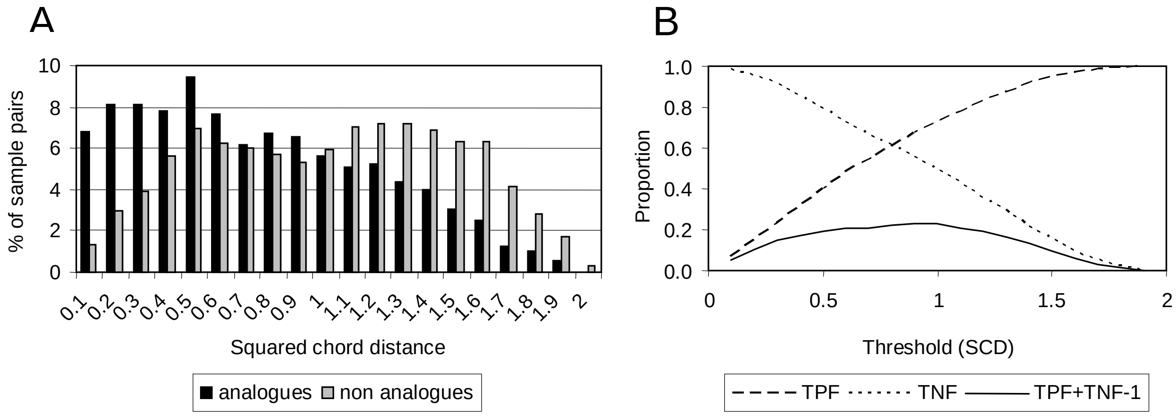

Figure 2. A) The distribution of SCD between pairs of surface pollen samples within the same vegetation communities (analogues) and between vegetation communities (non-analogues). B) Variation in sensitivity (TPF, true positive fraction) and specificity (TNF, true negative fraction) with the SCD threshold chosen to separate analogue from non-analogue sample pairs. The optimal threshold is found where the index TPF+TNF-1 is at a maximum (i.e. at SCD 1.0).

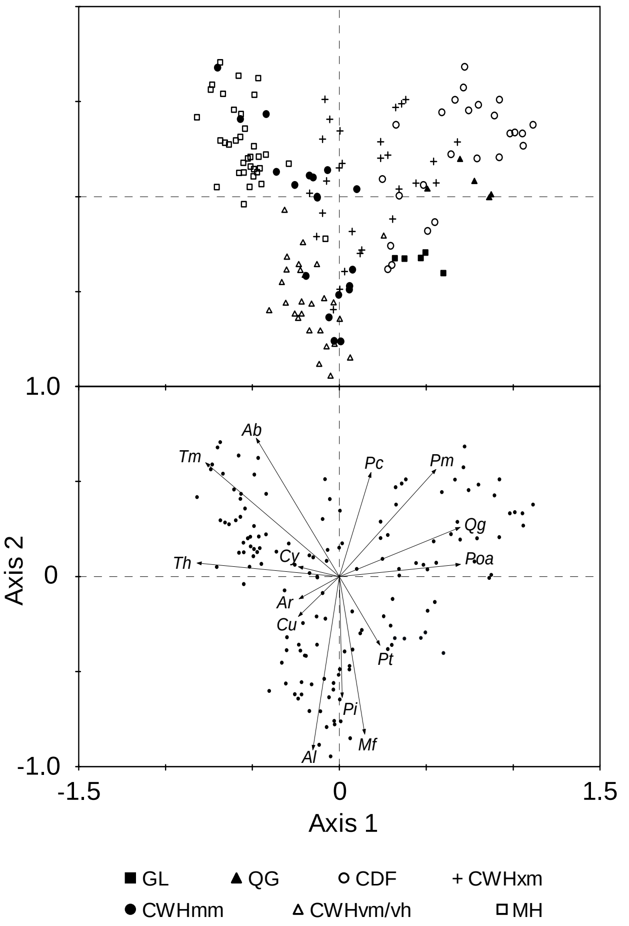

Figure 3. PCA plot showing the clustering of surface samples (top panel) and the species loadings for important pollen and spores from those samples (bottom panel). The abbreviations are as in Figure 1, with the additions of Ab=*Abies*, Al=*Alnus*, Ar=*Artemisia*, Cu=Cupressaceae, Cy=Cyperaceae, Mf=Monolete ferns, Pc=*Pinus contorta*, Pi=*Picea*, Pm=*Pseudotsuga menziesii*, Poa=Poaceae, Pt=*Pteridium*, Qg=*Quercus garryana*, Th=*Tsuga heterophylla* and Tm=*Tsuga mertensiana*.

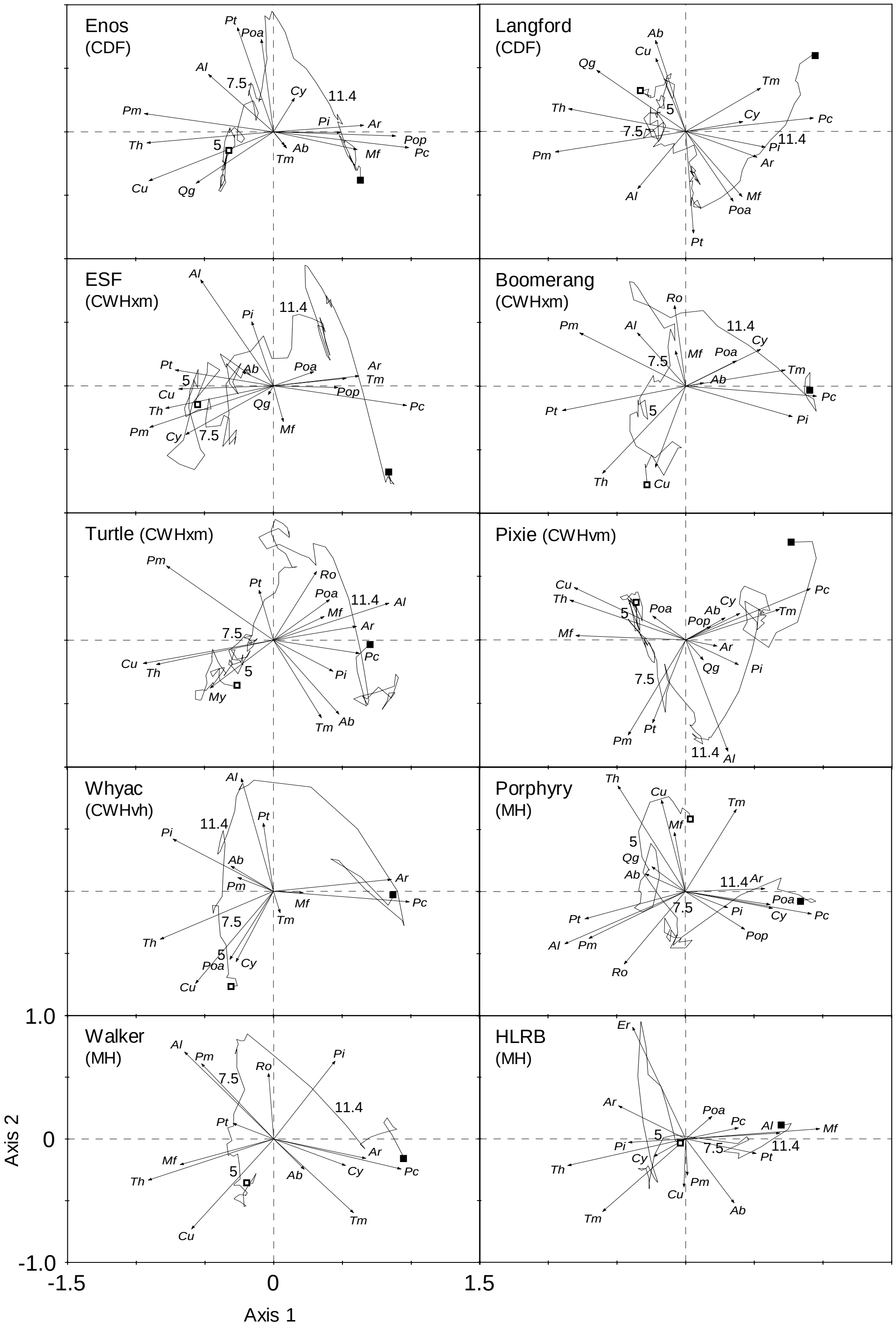

Figure 4. PCA plots of species loadings (vectors) for important pollen and spores from the sediment cores. Also shown are the sample scores in stratigraphic order (solid line). The solid line is reflective of the vegetation evolution at each site. The chronology is in kilo-annum calendar years (ka cal BP) as recorded by the numbers in the plots. The solid square marks the beginning of the record whereas the open square marks the end. BEC zones are listed in parenthesis. The abbreviations are as in Figure 3, with the additions of Er=Ericaceae, Ro=Rosaceae and Pop=*Populus*.

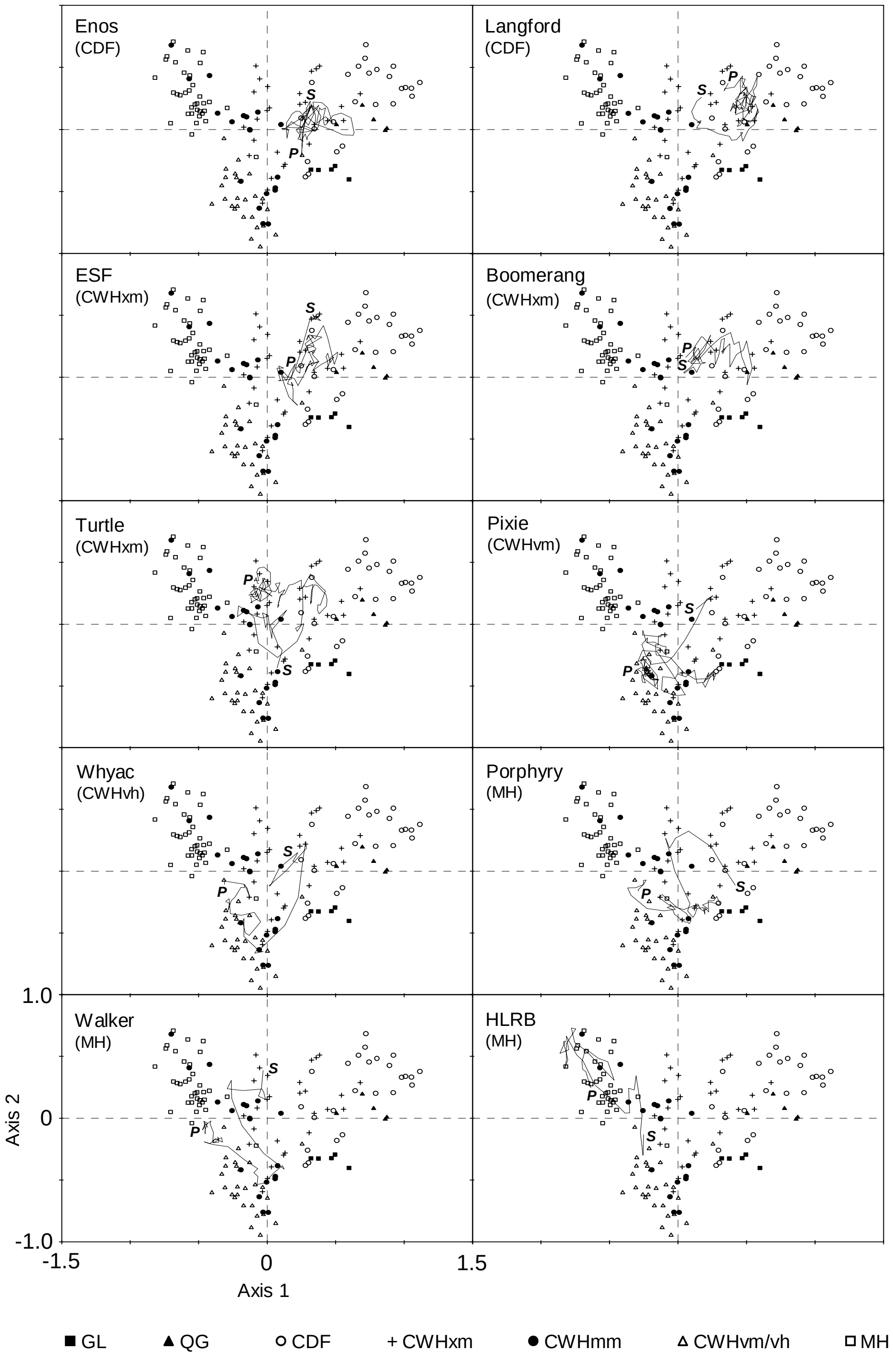

Figure 5. Plots of fossil samples in stratigraphic order (solid line) within the PCA of the modern surface spectra. The solid line only spans the Holocene, with S marking the start of the Holocene and P reflecting present-day. BEC zones are listed in parenthesis and the abbreviations are listed in Figure 1.

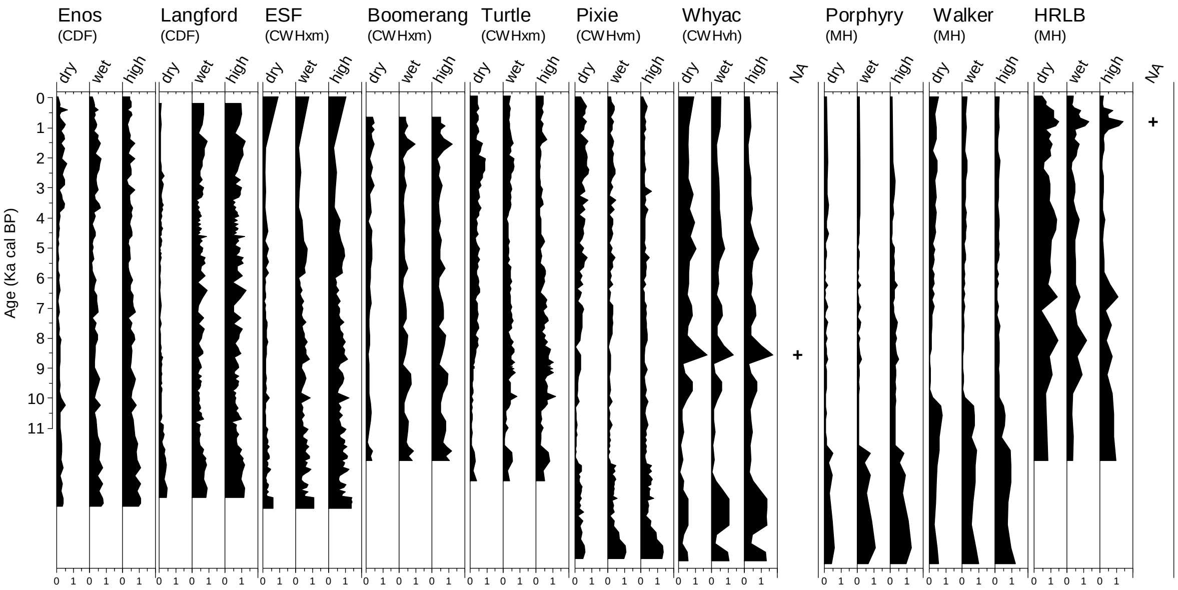

Figure 6. Dissimilarity plot showing the average SCD of each fossil sample to the five closest modern analogues within three groups of surface samples from Vancouver Island: CDF-CWHxm (the columns labeled dry); CWHmm-CWHvm/vh (labeled wet) and MH (labeled high). NA refers to non-analogous samples, defined as having a minimum SCD above 1.0. The Y-axis lists age only until 11,000 years ago, as the chronology before then is less certain because of extrapolation of radiocarbon dates.

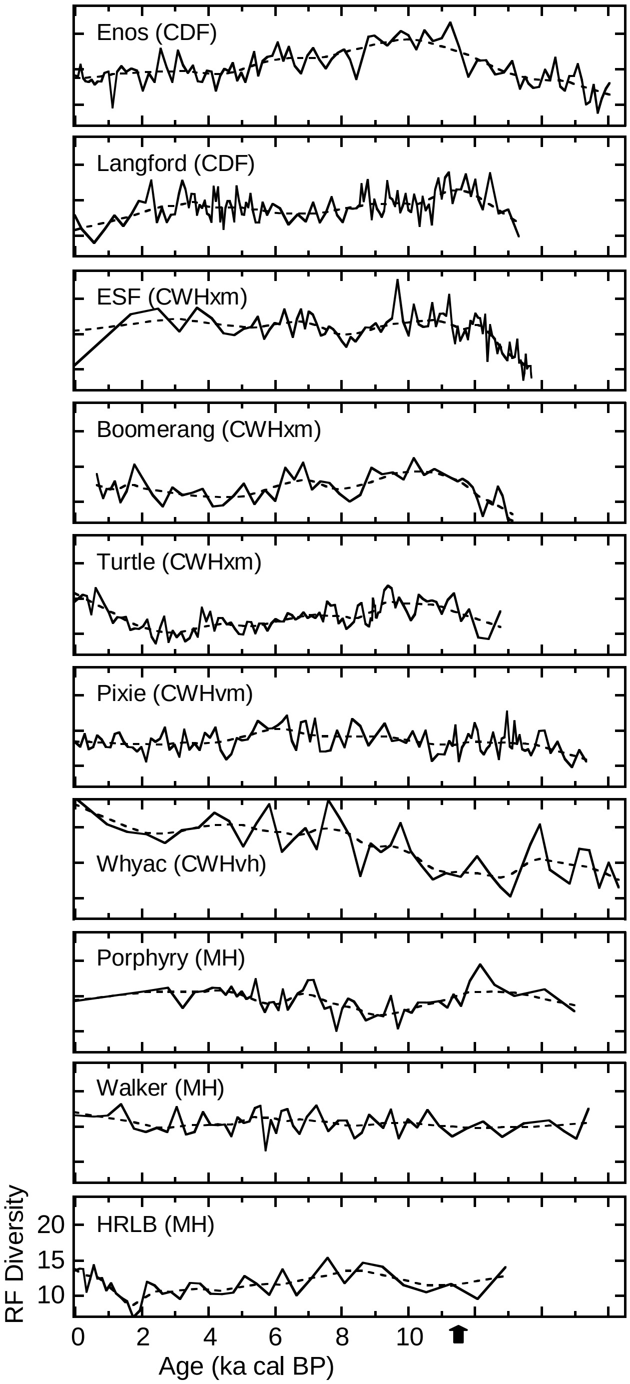

Figure 7. Rarefaction pollen richness curves for the sediment cores. The arrow marks the start of the Holocene 11,500 years ago. Due to poor basal age constraints, the chronology is not listed for the late-glacial interval. The dashed lines are smoothed curves.