
A multi-proxy peat study of Holocene vegetation history, bog development and carbon accumulation on northern Vancouver Island, Pacific coast of Canada

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Title: A multi-proxy peat study of Holocene vegetation history, bog development and carbon accumulation on northern Vancouver Island, Pacific coast of Canada

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Abstract

We present a multi-proxy paleoenvironmental study on a 10,400 cal yr peat sequence from an ombrotrophic bog in coastal British Columbia, Canada. Pollen, non-pollen palynomorph, plant macrofossil, and physicochemical analyses (bulk density, %C, %N, $\delta^{13}C$ and $\delta^{15}N$ isotopes) were used to document changes in vegetation, bog development, and carbon and nitrogen accumulation. Pollen assemblages indicate that regional vegetation in the warm, relatively dry early Holocene was mixed coniferous forest with scattered *Pseudotsuga menziesii*. Herbaceous peat with a C:N of ~28, combined with *Nuphar* microfossils and relatively high %N, suggest the presence of a herb-dominated peatland with standing water and/or bog pools. Carbon and nitrogen accumulation were at their highest during this early Holocene period at mean rates of 30.6 and 1.2 $g/m^2/cal$ yr, respectively. By 8000 cal yr BP and under a cooler, wetter climate, northern Vancouver Island supported *Tsuga heterophylla* rainforest similar to today. Decreasing relative water table, inferred from testate amoebae and fungal remains, facilitated the establishment of a *Sphagnum* bog by 8000 cal yr BP with abundant ericaceous shrubs after 5000 cal yr BP. Temporal variation in carbon accumulation rates correspond with changes in plant functional types and hydrological conditions: rates were lowest in the early to mid-Holocene during accumulation of *Sphagnum* peat (7.1 $g/m^2/cal$ yr) and increased in late Holocene ligneous peat (12.4 $g/m^2/cal$ yr). Our multi-proxy approach demonstrates the overarching control of climate on bog development and carbon and nitrogen accumulation, with seasonality likely playing a major role, but also highlights the strong influence of autogenic processes at a local scale.

Keywords

peat, pollen, non-pollen palynomorphs, C:N ratio, carbon and nitrogen accumulation, Procrustes analysis

Introduction

Peatlands provide excellent records of ecological and environmental change on long timescales, as slow rates of decay relative to primary production promote the accumulation of peat and exceptional preservation of fossil material (Charman, 2002; Rydin and Jeglum, 2013). Peatlands are also important long-term sinks for carbon dioxide, storing more carbon (C) per unit area than any other terrestrial ecosystem, and major sources of atmospheric methane (Gorham, 1991; Frolking and Roulet, 2007; Limpens et al., 2008; Baird et al., 2009; Korhola et al., 2010). Climate is the dominant macroscale control on peatland development and long-term C accumulation, with both temperature and precipitation playing important roles in primary production and decay (e.g., Clymo et al., 1998; Baird et al., 2009). Loisel et al. (2014) compiled a large database of Holocene C accumulation rates from northern peatlands that demonstrates that, at large spatial scales, the highest C accumulation rates occurred during the early Holocene, when northern latitudes were characterized by relatively high summer insolation and greater seasonality (Berger and Loutre, 1991). In another large compilation, Charman et al. (2013) show the dominant control of climate during the last millennium: in northern peatlands, C accumulation was higher during the warm Medieval Climate Anomaly than during the Little Ice Age. At an individual site, however, local-scale factors such as topography, hydrology, species composition, and disturbance can act as principal controls on peatland dynamics and C accumulation (e.g., Turunen and Turunen, 2003; Magnan and Garneau, 2014; Shiller et al., 2014). In order to better understand the effects of climate change on peatlands and their role in global change, as well as the importance of local autogenic processes, more research is needed on past peatland dynamics, long-term C accumulation, and connections to changes in vegetation, hydrology and climate, particularly in regions where peat studies are lacking.

Peatlands are common in Pacific Canada, particularly on the hypermaritime north coast of British Columbia (BC), where wetlands cover up to 75% of the terrestrial landscape (National Wetlands Working Group, 1988). Most of these are peatlands that form on flat to moderately sloping terrain. Mild temperatures, high precipitation and abundant fog sustain these wetlands, reduce decomposition, and promote the accumulation of peat (Asada and Warner, 2005). Paleoecological studies conducted in coastal BC bogs (e.g., Heusser, 1960; Hebda, 1983; Banner et al., 1983; Brown and Hebda, 2002) have focussed primarily on reconstructing Holocene vegetation dynamics from fossil pollen assemblages. Recently, Huntley et al. (2013) combined pollen and non-pollen palynomorphs to assess the impact of climate change and recent human activity on vegetation and bog development over the last 1800 cal yr on Haida Gwaii (Queen Charlotte Islands, BC). Turunen and Turunen (2003) provide the only study in coastal BC that documents changes in %C and %N in a Holocene peat record and infers long-term rates of C accumulation. Based on n=12 samples spanning the last 8500 cal yr, they found a relatively low mean rate of C accumulation (8.6 g/m^2/cal yr, as reported by Loisel et al., 2014), with the highest C accumulation rates occurring in the early Holocene. Given the abundance of wetlands and specifically peat-accumulating bogs in Pacific Canada, there is a need for more research aimed at understanding bog development and peat C accumulation in this maritime region. The coastal perspective is important as it offers an opportunity to examine whether peatlands on the north

Pacific coast have lower C accumulation relative to continental sites, as has been addressed elsewhere (Yu et al., 2009, 2014). Despite abundant precipitation and mild temperatures year-round that result in long growing seasons, oceanic bogs generally accumulate less peat and store less C than continental peatlands because the high primary production is offset by high decomposition (Malmer and Wallen, 1993; Asada and Warner, 2005). In fact, Gorham et al. (2003) noted a strong negative relationship between long-term rates of peat accumulation and precipitation in North American peatlands. Thus, we expect sites in coastal BC to have relatively low rates of peat accumulation and C sequestration compared to regions where seasonality in temperature is greater and precipitation is less abundant.

Here, we present a multi-proxy study of a peat sequence from an ombrotrophic bog on northern Vancouver Island, BC aimed at understanding how changes in ecological, hydrological and environmental conditions over the Holocene relate to long-term rates of C and N accumulation. Fossil pollen and plant macrofossils are used to document regional and local changes in vegetation communities and infer past environmental conditions. Bog development, edaphic conditions, and relative water table depth are also inferred from non-pollen palynomorphs i.e., testate amoebae, fungal and algal remains, and aquatic plant microfossils. Physicochemical proxy records (i.e., bulk density, %C and %N content, $\delta^{13}C$ and $\delta^{15}N$ isotopes) are used to further document the bog's history including changes in plant functional groups, nutrient status and peat decomposition. Finally, long-term rates of C and N accumulation are compared to vegetation and hydro-climatic changes over the Holocene. This multi-proxy approach allows for a more detailed record of bog dynamics from coastal BC than achieved in previous studies as well as the opportunity to evaluate concordance between different peat-based proxy records. This study also helps to clarify the relationship between long-term rates of peat accumulation and precipitation, and aids in the understanding of how climate, hydrology and vegetation interact to shape peatlands and C accumulation in oceanic settings.

Materials and methods

The study site (50° 34’ 21” N, 127° 04’ 20” W; 93 m asl) is a flat ombrotrophic bog located near the town of Port McNeill on northeastern Vancouver Island (Figure 1). Port McNeill Bog (informal name) lies within the Suquash Basin, an area of particularly low relief (<350 m) within extensive lowlands that span northern Vancouver Island, the mainland coast of British Columbia and northeastern Haida Gwaii (Queen Charlotte Islands). The region supports temperate coniferous rainforest with bog-forest complexes under a cool, humid climate. Mean summer temperature is 13.7°C and mean winter temperature is 4.1°C (Port Hardy Airport weather station; Environment Canada, 2014). Mean annual precipitation is 1908 mm/yr, with most precipitation falling as rain between September and April.

[INSERT FIGURE 1]

The summer water table depth at Port McNeill Bog (PMB) is ~20 cm (this study; Howie and van Meerveld, 2013), which approximates the current depth of the acrotelm-catotelm interface (Clymo, 1984). The plant community is in advanced succession, dominated by ericaceous shrubs (i.e., *Rhododendron groenlandicum* [formerly *Ledum groenlandicum*], *Empetrum nigrum*, *Vaccinium uliginosum* and *Kalmia microphylla* ssp. *occidentalis*) and two species of *Sphagnum* moss (*S. capillifolium* and *S. fuscum*). Other common species include *Rubus chamaemorus*, *V. oxycoccus*, *S. papillosum*, *S. pacificum* and *Pleurozium schreberi* as well as stunted *Pinus* *contorta* var. *contorta* trees. *Gaultheria shallon*, *Eriophorum chamissonis*, *Cornus unalaschkensis*, *Drosera rotundifolia* and *Juncus ensifolius* occur infrequently. Open *P. contorta* bog-woodland with *Tsuga heterophylla* and *Thuja plicata* surround the bog.

In July 2012, a 3.24 m peat core was collected from PMB using a side-filling 'Russian' sampler. Overlapping sections were retrieved from two parallel boreholes located 50 cm apart. After retrieval, the peat was stored at 4°C at the University of Victoria. Seven AMS radiocarbon ages (^{14}C yr BP) were obtained, each of which was on a single, small fragment of wood (Table 1), and calibrated to calendar years (cal yr BP) using the IntCal13 calibration dataset from Reimer et al. (2013). A chronology based on these ages and –62 cal yr BP for the top of the core was fit using a Stineman interpolation (Stineman, 1980) with the 'stinepack' (Johannesson and Bjornsson, 2012) and 'clam' (Blaauw, 2010) packages in R (R Core Team, 2014). Stineman interpolation is similar to simple linear interpolation in that the age-depth model is forced through the best available estimates of age i.e., the calibrated ^{14}C ages (Telford et al., 2004), but it stabilizes slopes near ^{14}C ages, providing a more robust estimate of mean accumulation rates over long timescales. Thus, Stineman interpolation helps to avoid the unrealistic assumptions of simple linear interpolation that accumulation is constant between ages and that accumulation rates change abruptly and precisely at dated depths in a sequence. A Bayesian approach to age-depth modeling using the 'Bacon' package (Blauuw and Christen, 2011) was also considered. The 'Bacon' age model is nearly identical to the interpolation methods for most time intervals and the Stineman model sits entirely within the 95% confidence intervals of the 'Bacon' model; however, in our case, 'Bacon' forces the age-depth model towards the edge of the 2σ calibration range for the ^{14}C age at 140 cm, producing a lower change in accumulation rate for a portion of the peat core where ash-free bulk density measurements suggest a larger change in accumulation rate. Changing the default prior information in 'Bacon' results in an even more problematic age-depth model: the ^{14}C age at 140 cm is ignored and accumulation rates between 124 and 235 cm, which accounts for ~3700 cal yr, are more or less constant, despite important changes in peat type.

Peat subsamples (1-2 cm^3) were prepared for pollen and non-pollen palynomorph (NPP) analyses using 10% HCl, 10% KOH and acetolysis solution, and then mounted in 2000 cs silicone oil. Samples were not treated with hydrofluoric acid. One tablet of 18,684 ± 371 *Lycopodium* spores (Batch No. 177745) was added to each sample to estimate pollen and NPP concentrations. Before chemical treatment, each sample was sieved at 150 μm and the larger fraction was retained for peat composition analysis. A minimum of 350 terrestrial pollen and spores was identified in each sample using dichotomous keys (e.g., McAndrews et al., 1973; Kapp et al., 2000) and reference material at the University of Victoria. *Alnus* pollen were differentiated into *Alnus rubra* and *Alnus viridis* types following May and Lacourse (2012). Identification of Ericaceae pollen was aided by Warner and Chinnappa (1986) and local reference material; however, most Ericaceae pollen from this site could not be differentiated below the family level due to overlapping pollen morphologies (Warner and Chinnappa, 1986; Lacourse, unpublished data). Non-pollen palynomorphs including testate amoebae tests, fungal spores and hyphopodia, aquatic plant microfossils, and algal remains were identified on the same slides used for pollen analysis, using various sources including van Geel (1978), Pals et al. (1980), Kuhry (1997), Charman et al. (2000), Marrotte et al. (2012) and Payne et al. (2012).

Pollen percentages were calculated using the sum of all terrestrial pollen and spores, excluding pollen from obligate aquatic species and *Sphagnum* spores. Numerical zonation of the pollen and NPP data was based on taxa that exceeded 1% of the sum and conducted using optimal splitting by information content (Bennett, 1996), although binary splitting and constrained cluster analysis produced identical results. Statistical significance of the resulting zones was tested using broken stick models. Procrustes analysis (Peres-Neto and Jackson, 2001) was used to assess the degree of congruence in the major variation of the pollen and NPP datasets. Procustes was conducted on the sample scores of independent principal component analyses of the two datasets using the 'vegan' package (Oksanen et al., 2013) in R. The significance of the Procrustes correlation statistic (r), which quantifies the similarity of the two matrices, was tested using 9999 permutations.

To estimate the major macrofossil components of the peat and relative changes with depth, we analyzed the >150 μm fraction of each 1-2 cm^3 pollen sample using an approach similar to the quadrat method of Barber et al. (1994) and Mauquoy et al. (2010). The >150 μm fraction was poured into gridded petri dishes and all macrofossils in 15 randomly selected 1 × 1 cm quadrats were differentiated into major peat components (i.e., herbaceous material, moss stems/leaves Ericaceae roots and leaves, and unidentifiable organic material) and are expressed as percentages of the total count from those quadrats. Seeds, *Nuphar* sclereids (>150 μm), and charcoal fragments (>150 μm) are presented as the total number encountered in those same quadrats.

Loss-on-ignition (LOI) was used to estimate organic matter content (%) of the peat (Dean, 1974; Heiri et al., 2001). Peat samples of 2 cm^3 were taken at 2-cm intervals along the peat core (*n*=163), dried at 105°C for 20 h, and then ignited at 550°C for 4 h. Ash-free bulk density (AFBD) was calculated as the dry weight (g) divided by the wet volume (cm^3) and then multiplied by % organic matter content. For C and N analyses, an additional 2 cm^3 from the same depths (*n*=163) was dried to constant mass at 70°C for 20 h and ground to a fine powder (<125 μm) using a ball mill. C and N contents and $\delta^{13}C$ and $\delta^{15}N$ isotopes were determined on 3-5 mg of dried homogenized peat in 5 × 8 mm tin capsules using a Costech ECS 4010 thermal combustion elemental analyzer attached to a Thermo Finnigan DELTA^{Plus} Advantage isotope ratio mass spectrometer at the University of Victoria. Replicate analyses were performed on 19 of the 163 samples. C and N isotope data are reported in conventional δ (‰) notation with reference to Vienna Pee Dee Belemnite (VPDB) carbonate and atmospheric nitrogen (air), respectively. Analytical reproducibility of the mass spectrometer was assessed using acetanilide (71.09% C and 10.36% N) and caffeine (–42.22‰ $\delta^{13}C$ and –0.94‰ $\delta^{15}N$) standards included in every run. Relative uncertainties calculated from analyses of these standards are better than ±0.1% and ±1.5% for %C and %N, respectively, and ±0.27‰ and ±0.09‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Carbon (CAR; g/m^2/cal yr) and nitrogen (NAR; g/m^2/cal yr) accumulation rates were calculated using %C and %N, respectively, along with AFBD (g/cm^3) and modeled deposition times (cal yr/cm). Mean CAR and NAR are weighted by the deposition time of each sample.

Results

Chronology, peat stratigraphy and plant macrofossils

The age-depth model for the PMB peat core (Figure 2) predicts an age of 10,413 cal yr BP for the base of the core i.e., at 324 cm. Modeled accumulation rates vary between 0.01 and 0.08

cm/cal yr, with a mean deposition time of 32 cal yr/cm. Deposition times are notably higher during two intervals (140-124 and 64-34 cm), indicating slower net peat addition ~7100–5400 cal yr BP and ~2900–800 cal yr BP, respectively. The overall age-depth relationship is convex with decreasing peat accumulation rates through time. This is in contrast to the concave pattern of peat accumulation in other oceanic settings (Clymo, 1984).

[INSERT FIGURE 2]

The basal portion of the peat core (324-171 cm; ~10,410-7960 cal yr BP) consists of fibrous herbaceous peat (Figure 3) with Cyperaceae leaves and achenes and abundant *Nuphar* sclereids (>150 µm), most likely derived from *N. polysepala*. Unidentifiable organic material accounts for ~20% of the peat composition. *Sphagnum* and Ericaceae remains, and fern sporangia were encountered infrequently in this portion of the core. *Nuphar* sclereids (>150 µm) decrease dramatically after 8000 cal yr BP, although they continue to be present in trace amounts until ~4400 cal yr BP. The herbaceous peat is sharply overlain by *Sphagnum* peat (171-122 cm; ~7960-5270 cal yr BP) that is dominated by *Sphagnum* leaves and stems and includes minor components of Ericaceae roots and leaves and less overall unidentifiable organic material. *Juncus* seeds first appear ~7900 cal yr BP and continue to be present in low numbers for the remainder of the record. There is a gradual transition to *Sphagnum*-ligneous peat (122-97 cm; ~5270-4150 cal yr BP), where *Sphagnum* leaves/stems and Ericaceae roots each account for ~35% of the peat composition. Ligneous peat (*sensu* Troels-Smith, 1955) that consists primarily of Ericaceae roots and unidentifiable organic material, with occasional peaks in *Sphagnum* remains, occurs from 97 to 30.5 cm (~4150-680 cal yr BP). The uppermost 30.5 cm is composed of a mixed moss-ligneous peat, marked by an increase in the relative abundance of brown mosses, primarily *Drepanocladus* cf. *exannulatus*. No distinct charcoal layers or horizons are present in the PMB core; however, macroscopic charcoal (Figure 3) is abundant between 121 and 32 cm (~5220-730 cal yr BP). Charcoal concentrations are highest between 68 and 44 cm (~3070-1510 cal yr BP).

[INSERT FIGURE 3]

Pollen and spore assemblages

Fossil pollen and spores were identified in 66 peat samples with a mean temporal resolution of 160 cal yr between samples. Numerical zonation of the pollen and spore percentage data returned two major pollen and spore assemblage zones (Figure 4). The major pollen zone boundary at ~8000 cal yr BP corresponds with the stratigraphic change from herbaceous peat to *Sphagnum* peat at 171 cm. Overall trends in pollen and spore percentages correspond closely with changes in taxa-specific pollen concentrations with a few exceptions, which are noted below.

[INSERT FIGURE 4]

Pollen Zone 1 (~10,410-7960 cal yr BP) is characterized by high percentages of *Alnus rubra*, *Tsuga heterophylla* and *Picea sitchensis*, with *A*. *rubra* decreasing through Pollen Zone 1b (Figure 4). *Tsuga heterophylla* increases in relative abundance from ~20% to 50% of the pollen sum; however, *T. heterophylla* pollen concentrations remain relatively constant at about 19,000 grains/cm^3. *Pinus contorta* type is present at <10% and *Pseudotsuga menziesii*, *Abies* and Cupressaceae each account for <2%. *Sphagnum* spores and Ericaceae pollen first appear at ~10,000 and 9200 cal yr BP, respectively. Pollen from herbaceous taxa are infrequent throughout the record with Cyperaceae accounting for ~1% in Pollen Zone 1 and remaining relatively constant at <2% for the entire record. Fern spores including *Pteridium aquilinum* and *Athyrium filix-femina* make up ~5% of the sum in this basal zone. *Nuphar* pollen is at its highest relative abundance (i.e., 2-5%) with a notable decrease in concentration after 9600 cal yr BP.

In Pollen Zone 2 (7960 cal yr BP to present), *T. heterophylla* is the dominant pollen type (~40-70%) and has a higher mean pollen concentration (~35,000 grains/cm^3) than in the preceding zone. *Picea sitchensis*, *A. rubra* type and *P. contorta* type continue to be present at 5-10% each. *Abies* and Cupressaceae are higher than in Pollen Zone 1, but remain at <5% throughout the entire record. Ericaceae pollen including *Ledum* type increases to ~5-25% in Pollen Zone 2a and then become co-dominant with *T. heterophylla* in Pollen Zone 2b, with Ericaceae pollen accounting for 20-60% of the total sum. The abundance of *Sphagnum* spores varies between 2 and 30% with the largest increase occurring at 3000 cal yr BP, when spore concentrations reach 52,000 spores/cm^3. Pteridophyte spores including *Polypodium* account for <2%. There is a single tetrad of *Drosera* pollen at ~5200 cal yr BP. *Alnus rubra* type increases to almost 40% in the uppermost sample, but its concentration (~21,000 grains/cm^3) is far less than in Pollen Zone 1a (~53,000 grains/cm^3). *Pinus contorta* type concentrations between 3500 cal yr BP and the present are similar to those in the earliest Holocene (Pollen Zone 1a).

Testate amoebae, fungal remains and other non-pollen palynomorphs

A total of 19 different non-pollen palynomorphs (NPP) were identified on the same slides used for pollen analysis. Procrustes analysis demonstrated a significant correlation (r=0.637, $P <$ 0.0001) between the pollen and NPP datasets. The strength of the correlation is driven primarily by highly correlated variation on Procrustes axis 1 (r=0.814) and less so by variation on axis 2 (*r*=0.461). Numerical zonation of the NPP dataset identified three statistically significant biostratigraphic zones (Figure 5).

Nymphaeaceae leaf hair basal cells are the most abundant NPP in NPP Zone 1 (~10,410 to 7600 cal yr BP) with a concentration of 65,000 cells/cm^3 near the base of the record followed by decreasing concentrations after 9600 cal yr BP (Figure 5). *Nuphar* sclereids (<150 μm) follow the same general trend, decreasing through this zone until no longer present after 8250 cal yr BP. Single occurrences of *Mougeotia* and *Closterium idiosporum* algal zygospores occur in a few samples in this zone. Testate amoebae are minor components of the NPP record until the middle of NPP Zone 1, when *Arcella hemisphaerica* appears at ~9200 cal yr BP and then increases to ~3500 tests/cm^3. *Amphitrema flavum* appears in the record at the same time and increases in concentration immediately before NPP Zone 2. Fungal remains are at low concentrations in NPP Zone 1 with *Gaeumannomyces* hyphopodia consistently present. *Gelasinospora*, cf. *Entophlyctis lobata*, *Helicoon pluriseptatum* and Microthyriaceae are present in the upper portion of NPP Zone 1.

[INSERT FIGURE 5]

NPP Zone 2 (7600 to 4480 cal yr BP) is dominated by *Amphitrema flavum*, which reaches a maximum of 12,700 tests/cm^3 at ~4900 cal yr BP before disappearing at the boundary to NPP Zone 3. *Hyalosphenia subflava* tests are present in low concentrations (<2000 tests/cm^3). *Assulina muscorum* is also common and single occurrences of *A. seminulum* occur in two samples in this zone. *Gaeumannomyces* and *Gelasinospora* continue to be present and cf. *Entophlyctis lobata*, *H. pluriseptatum* and Microthyriaceae increase relative to NPP Zone 1.

Hyalosphenia subflava testate amoebae dominate NPP Zone 3 (4480 cal yr BP to present), with a mean concentration of 12,000 tests/cm^3 that excludes the peak at ~400 cal yr BP, where the concentration reaches 162,500 tests/cm^3. *Assulina muscorum* is present in the uppermost samples and *Cyclopyxis arcelloides* type, most likely belonging to *Cyclopyxis* due to its smooth-rimmed and invaginated aperture, appears in the top two samples, reaching 4500 tests/cm^3. *Gaeumannomyces* hyphopodia and *Gelasinospora* ascospores are at their highest concentrations in this zone, although *Gelasinospora* decreases to trace amounts in the last 1500 cal yr. Microthyriaceae, cf. *Entophlyctis lobata*, and *Helicoon pluriseptatum* are also present in NPP Zone 3, except between ~4000 and 2000 cal yr BP when *Gelasinospora* ascospores are abundant.

LOI, bulk density, C and N analyses

The mean temporal resolution of the physicochemical records is 64 cal yr between samples with a range of 14 – 275 cal yr. Water content of the PMB core is 90%, on average, with organic matter content accounting for nearly all of the remaining material i.e., 95.6 to 99.9% loss-on-ignition (Figure 6). Mean AFBD is 0.09 g/cm^3 with values ranging between 0.05 and 0.16 g/cm^3 (Figure 6). Variation in AFBD corresponds with stratigraphic changes in peat type (Figure 3), with relatively high bulk density (~0.11 g/cm^3) in late to mid-Holocene ligneous peat, low bulk density (~0.07 g/cm^3) in mid- to early Holocene *Sphagnum* peat and intermediate values (~0.09 g/cm^3) in the earliest Holocene herbaceous peat, in agreement with values for different peat types compiled by Loisel et al. (2014).

[INSERT FIGURE 6]

More or less synchronous changes are observed in %C and %N, corresponding with changes in peat type (Figure 6). Mean C content is 55.5% with variation between 47.7% and 61.5% (Figure 6); these values agree with or exceed those found in northern peatlands (Loisel et al., 2014). In most samples, %C exceeds the mean C content of peat organic matter in western Canada (i.e., 51.8%; Vitt et al., 2000) that is routinely used to infer peat C accumulation from bulk density (e.g., Yu et al., 2014). The early to mid-Holocene *Sphagnum* peat and the uppermost moss-ligneous peat are characterized by relatively low %C (52% on average), whereas the basal herbaceous peat and the mid-Holocene ligneous peat have ~57% C. Mean N content is 1.4% and is relatively high (~2.1%) in early Holocene herbaceous peat and low (~0.7%) in the early to mid-Holocene *Sphagnum* peat with increasing values (~1%) towards the present. Accordingly, C:N varies considerably: mean values in the herbaceous, *Sphagnum* and ligneous peats are 28, 90 and 67, respectively.

As expected, changes in δ^{13}C and δ^{15}N isotopes also follow stratigraphic changes in peat type (Figure 6). δ^{13}C is highest in the *Sphagnum* and moss-ligneous peats with mean values of –26.6‰ and lowest in the ligneous and herbaceous peats, where mean values are –27.6‰. There is a weak positive correlation ($r=0.38$, $P<0.001$) between δ^{13}C and C:N, suggesting that diagenesis may have played some role in altering δ^{13}C values, particularly in the mid- to early Holocene *Sphagnum* peat where the correlation is stronger ($r=0.57$, $P<0.001$). δ^{15}N reaches up to 3.7‰ in the late to mid-Holocene ligneous peat, is low in the preceding *Sphagnum* peat (~–3.9‰) and intermediate in the early Holocene herbaceous peat (~–2.3‰). There is no correlation between δ^{15}N and C:N ($r=–0.09$, $P=0.254$).

Carbon accumulation rates (CAR) are 16.1 g/m^2/cal yr, on average, and vary between 2.4 and 48.7 g/m^2/cal yr, following changes in peat stratigraphy (Figure 7). CAR is highest in the early Holocene herbaceous peat (mean = 30.6 g/m^2/cal yr), gradually decreasing to low rates ~7000–5500 cal yr BP during accumulation of *Sphagnum* peat. In the mid- to late Holocene, CAR increases with accumulation of ligneous peat, although rates are somewhat lower ~2000-900 cal yr BP. CAR is marked by an increase in the uppermost peat that is likely related to low decomposition in the acrotelm. The time-weighted mean nitrogen accumulation rate (NAR) is 0.41 g/m^2/cal yr. NAR is highest (mean = 1.15 g/m^2/cal yr) in the earliest Holocene and lowest (mean = 0.11 g/m^2/cal yr) during accumulation of *Sphagnum* peat in the mid-Holocene (Figure 7). Because CAR and NAR are both calculated using peat accumulation rates (Figure 2) and ash-free bulk density (Figure 6), NAR follows the same temporal trend as CAR (Figure 7).

[INSERT FIGURE 7]

Discussion

Holocene vegetation history on northern Vancouver Island

Pollen records from northern Vancouver Island (Hebda, 1983; Hebda and Haggarty, 1997; Lacourse, 2005), the adjacent mainland coast (Stolze et al., 2007; Galloway et al., 2007, 2009), and the exposed continental shelf at Cook Bank (Lacourse et al., 2003) demonstrate that the region supported open *Pinus contorta* woodland soon after deglaciation, which occurred ~16,500 cal yr BP in this region (Howes, 1981; Hebda, 1983; Luternauer et al., 1989). With increasing temperatures (Heusser et al., 1985), open *Pinus*-dominated communities were followed by mixed coniferous forests that included *Picea sitchensis*, *Tsuga mertensiana* and *T. heterophylla*, species with higher relative shade tolerance, longer lifespans and slower relative growth rates (Lacourse, 2009). At some sites, the cool Younger Dryas is marked by increases in the abundance of *Tsuga mertensiana* (e.g., Mathewes, 1993; Lacourse, 2005; Stolze et al., 2007).

At Port McNeill Bog (PMB), the pollen record begins at ~10,400 cal yr BP (Figure 4) during mixed coniferous forest that characterized much of coastal BC in the early Holocene (e.g., Heusser, 1960; Hebda, 1983; Stolze et al., 2007; Galloway et al., 2009). Until about 8000 cal yr BP, forests on northern Vancouver Island were composed primarily of *T. heterophylla*, *P. sitchensis* and *Alnus rubra* and were likely somewhat more open than at present, as indicated by abundant Polypodiaceae ferns including *Pteridium aquilinum. Alnus* pollen can be overrepresented in modern pollen assemblages compared to its abundance in nearby plant communities (e.g., Allen et al., 1999). Therefore, it is possible that the abundant *A. rubra* pollen at PMB in the early Holocene may reflect, at least in part, regional pollen transport linked to high pollen production and effective wind dispersal; however, modern pollen assemblages similarly dominated by *T. heterophylla*, *P. sitchensis* and *A. rubra* have been retrieved from lowland lakes in *P. sitchensis*-dominated forest to the south in coastal Washington (Heusser, 1978; Gavin et al., 2005). Early Holocene pollen assemblages at PMB are nearly identical to those at Misty Lake (Lacourse, 2005), located 14 km northwest of PMB (Figure 1), indicating that pollen assemblages from peat deposits at PMB provide a similar record of regional forest composition as those derived from nearby lake sediments.

Pseudotsuga menziesii was at its highest abundance in the PMB pollen record between 10,000 and 8250 cal yr BP, reaching a maximum of 4% (Figure 4). Because *P. menziesii* produces less pollen relative to other conifers and its pollen has a short dispersal distance (Tsukada, 1982), *P.*

menziesii pollen greater than 1-2% indicates its local presence in surrounding forests (Hebda, 1983; Heusser, 1978). Its local presence is confirmed by *P. menziesii* cone scales and seed wings in nearby lacustrine sediments that date to ~9300 cal yr BP (8300 ± 70 ^{14}C yr BP; GSC-2435 [Howes, 1981]). Today, *Pseudotsuga* is the dominant tree in forests on southeastern Vancouver Island, where the climate is significantly warmer and drier, but it is uncommon on northern Vancouver Island. Warm early Holocene summers permitted *P. menziesii* to migrate northward on Vancouver Island (this study; Hebda, 1983; Lacourse, 2005) and the adjacent mainland (Galloway et al., 2007). Once climate began to cool, the northern limit of *P. menziesii* retracted (Gugger and Sugita, 2010); by about 7200 cal yr BP, *P. menziesii* more or less disappears from the PMB pollen record. A decline in *P. menziesii* was observed at about the same time in the pollen record from nearby Misty Lake (Lacourse, 2005).

By 8000 cal yr BP, *Tsuga heterophylla* became the dominant tree species near PMB (Figure 4) and throughout the region (Hebda, 1983; Lacourse, 2005; Stolze et al., 2007; Galloway et al., 2007, 2009), forming forests along with *Picea sitchensis*, *Abies* and Cupressaceae. Increases in *Abies* and Cupressaceae, likely mostly derived from *Thuja plicata*, indicate an increasingly closed forest canopy, given their high shade tolerance (Lacourse, 2009). Climate was cooler and wetter on northern Vancouver Island than in the earliest Holocene, due to lower summer insolation and intensification of the Aleutian Low pressure system that allowed near-modern precipitation regimes to establish (Heusser et al., 1985; Brown et al., 2006). This cooler, wet climate facilitated the establishment of *Tsuga heterophylla*-dominated rainforest that continue to occupy much of the northeast Pacific coast today. The dramatic increase in *Alnus rubra* type pollen in the uppermost sample from PMB is likely associated with disturbance in surrounding forests, with commercial logging in the region beginning in the 1930s.

Local bog development near Port McNeill

The base of the PMB sequence is characterized by rapidly-accumulating herbaceous peat (Figures 2 and 3) with relatively high C content (~56%) and C:N ratios of ~25 (Figure 6) that are indicative of a terrestrial environment as opposed to a lake (Meyers and Teranes, 2001). However, *Nuphar* pollen, sclereids and basal cells (Figures 3-5) indicate the presence of standing water and/or bog pools necessary to support these aquatic plants. Analogous peat-accumulating wetlands with *Nuphar polysepala* occur in saturated low-lying areas in Pacific Canada (National Wetlands Working Group, 1988) and *N. polysepala*, often with erect aerial leaves as opposed to floating lily pads, occurs in shallow bog hollows and pools on Vancouver Island today (Golinski, 2004). Etnier and Villani (2007) showed that sclereids in *Nymphaea odorata* (Nymphaeaceae) confer structural support to aerial leaves and occur in higher frequency in the epidermis (rind) of aerial leaf petioles, compared to floating lily pads. The high abundance of *Nuphar* sclereids (Figures 3 and 5) in the basal peat at PMB may very well reflect the presence of such aerial leaves. The relatively high %N and low $\delta^{13}C$ (Figure 6) of this herbaceous peat also suggest the presence of shallow water and/or bog pools: peat that accumulates in aquatic settings tends to have higher %N and lower $\delta^{13}C$ due to the presence of aquatic plants and/or algal proteins and lipids that are typically N-rich and ^{13}C-depleted (Talbot, 2001; Meyers and Teranes, 2001; Jones et al., 2010).

The transition to a classic bog ecosystem begins with the appearance *Sphagnum* spores and Ericaceae pollen (Figure 4), as well as associated macrofossils (Figure 3), shortly after 10,000 cal yr BP. An increase in the abundance of *Arcella hemisphaerica*, a wet peatland testate amoeba (Markel et al., 2010; Payne et al., 2012), after 9200 cal yr BP and a corresponding increase in C:N ratios (Figure 6) as well as decreases in *Nuphar* remains (Figures 3-5) suggest shallowing of standing water and/or decreases in the extent of bog pools through the earliest Holocene. Increasing concentrations of fungal groups, which require oxic conditions to be major decomposers in peatlands (Wieder and Vitt, 2006; Rydin and Jeglum, 2013), also reflect the lowering of relative water table depths after ~8500 cal yr BP (Figure 5). It is difficult to uncouple climatic and non-climatic drivers of change at PMB during this interval and it is likely that both macroscale climate and local eco-hydrological processes played a role. The decreasing relative water table depth would have been facilitated by warm and relatively dry climate during the early Holocene as well as the rapid accumulation of peat, allowing bog vegetation i.e., *Sphagnum* mosses and Ericaceae shrubs to colonize the surface as the wetland dried up. A similar early Holocene transition from a shallow water wetland with *Nuphar* to a *Sphagnum* bog was also recorded at nearby Bear Cove Bog (Figure 1; Hebda, 1983). However, in bogs on the north coast of BC (e.g., Banner et al., 1983; Turunen and Turunen, 2003), paludification was the primary mode of development, with succession from wet minerotrophic coniferous forest to blanket bog woodland ecosystems in the early to mid-Holocene. These developmental pathways contrast with the swamp-fen-bog sequence typical of many boreal peatlands (Wieder and Vitt, 2006; Rydin and Jeglum, 2013).

A *Sphagnum*-dominated bog was fully established by 8000 cal yr BP, as shown by the abrupt stratigraphic change to *Sphagnum* peat (Figure 3), the abundance of *Sphagnum* leaves/stems, and increases in *Sphagnum* spores (Figure 4). A rapid transition to lower C and N content (~50% and 0.5%, respectively), but C:N ratios >100 (Figure 6) coincides with the change to *Sphagnum* peat and dominance by *Sphagnum* mosses, which although resistant to decay, have lower C and N content than vascular plants (Loisel et al., 2014). Furthermore, $\delta^{13}C$ values become more positive, reflecting peat accumulation above the water table, changes in surface vegetation and perhaps increased decomposition (Jones et al., 2010; Andersson et al., 2012).

Increases in Ericaceae roots and leaves (Figure 3) and pollen including *Ledum*-type (Figure 4) indicate that ericaceous shrubs also colonized the bog surface by 8000 cal yr BP. Fungi including *Helicoon pluriseptatum*, Microthyriaceae, and cf. *Entophlyctis lobata*, that are often associated with *Sphagnum* peat and to some extent ericaceous shrubs (e.g., Kuhry, 1997; Yeloff et al., 2007), also appear in the PMB record at about the same time (Figure 5) and changes in their concentrations correlate well with the varying abundance of *Sphagnum* remains (Figure 3). Testate amoebae during this time suggest variable hydrological conditions and/or the development of hummock-hollow surface topography. *Amphitrema flavum*, by far the most abundant testate amoeba between 7900 and 4700 cal yr BP, is one of the most common species in ombrotrophic peatlands and is generally found in wet conditions (Charman et al., 2000). *Assulina muscorum*, which can tolerate a wide range of conditions but is most abundant in intermediate to dry peatlands (Booth and Zygmunt, 2005; Charman et al., 2000; Payne et al., 2012), is also present. *Hyalosphenia subflava*, a testate amoebae indicative of dry conditions when in great abundance (Charman et al., 2000; Payne et al., 2012), also occurs in the mid-

Holocene, although it is far more abundant after 4000 cal yr BP, when ericaceous shrubs dominate the bog's vascular plant community and the water table continued to lower relative to the bog surface.

Around 5200 cal yr BP, Ericaceae macrofossils increase in relative abundance and by 4000 cal yr BP, PMB was dominated by ericaceous shrubs, as shown by the transition to ligneous peat (Figure 3) and the increase in Ericaceae pollen (Figure 4). *Pinus contorta* type pollen percentages increase around 3500 cal yr BP and, given a coincident increase in *Pinus* pollen concentrations, this likely reflects colonization of the bog surface by this species. As expected, bulk density and C and N contents (Figure 5) increase and C:N ratios decrease during accumulation of this ligneous peat and dominance by ericaceous shrubs, suggesting increased peat decomposition at this time. $\delta^{15}N$ transitions to more positive values after 4000 cal yr BP, reflecting a lower water table that allowed aerobic decay and ^{15}N-enrichment (Jones et al., 2010; Andersson et al., 2012). Lowering of the water table is also suggested by substantial increases in *Hyalosphenia subflava* (Payne et al., 2012) after 4000 cal yr BP (Figure 5). $\delta^{13}C$ decreases with the transition to an Ericaceae-dominated bog, which is likely related to a number of interacting factors including the change in plant functional types and increased microbial decomposition and summer moisture stress related to lowering of the water table. Given the cool, wet climate of the mid- to late Holocene, the increase in ericaceous shrubs and relative lowering of the water table appear to have been driven primarily by succession and autogenic processes rather than changes in climatic conditions.

The abundance of macroscopic charcoal increases fairly abruptly starting 5200 cal yr BP with the highest concentrations occurring 3000-1500 cal yr BP (Figure 5). The concentration of *Gelasinospora* ascospores, which are often associated with dry conditions and peat containing abundant charcoal (e.g., Kuhry, 1997; Yeloff et al., 2007; Chambers et al., 2011), follows the same general trend through time (Figure 5). Brown and Hebda (2002) suggest that because regional climate was cool and moist in coastal BC during the mid- to late Holocene, higher charcoal concentrations on southern Vancouver Island at this time may reflect the use of fire as a landscape management tool by local indigenous peoples. It is possible that small, low-severity fires were used at PMB to increase berry production in ericaceous shrubs, similar to that documented on Vancouver Island and elsewhere in BC during the historical period (Turner, 1999). Since no distinct charcoal layers were observed in the peat core from PMB, it is unlikely that fires were sufficiently severe to combust significant amounts of peat and/or the entire surface vegetation.

The mixed moss-ligneous peat in the uppermost portion of the PMB sequence (0-30.5 cm) may reflect changes in environmental conditions over the last 700 cal yr; however, because much of this peat sits above the current depth of the water table (20 cm) and therefore corresponds with lower decomposition in the acrotelm, we limit our interpretation of changes in the various proxies for this portion of the core. The uppermost peat is marked most notably by the increased relative abundance of *Drepanocladus* cf. *exannulatus*, a brown moss common in wet BC bogs that suggests an increase in surface wetness, potentially associated with recent land use changes adjacent to the bog. The increase in *Drepanocladus* is likely responsible for the decrease in %C in the uppermost peat, as brown mosses typically contribute less C to peat than vascular plants

(Loisel et al., 2014). With the increased abundance of brown moss in the uppermost peat and presumably a higher water table to support these mosses, $\delta^{13}C$ values increase to levels that are generally higher than in the mid-Holocene. *Assulina muscorum* and *Cyclopyxis arcelloides* type, testate amoebae that can tolerate varying levels of moisture (Charman et al., 2000; Booth and Zygmunt, 2005; Payne et al., 2012), also appear in the uppermost peat (Figure 5).

The abundance of *Sphagnum* spores (Figure 4) varies considerably after the bog established in the early Holocene and does not correspond with changes in the abundance of *Sphagnum* macro-remains or overall peat type (Figure 3). For example, *Sphagnum* spores reach a maximum abundance of ~30% between 3200 and 2700 cal yr BP during accumulation of ligneous peat as opposed to *Sphagnum* peat. Similarly, *Sphagnum capillifolium* and *S. fuscum* are abundant on the bog surface today, but *Sphagnum* spores are less than 4% in the uppermost peat. These differences suggest that the *Sphagnum* spore record from PMB does not accurately reflect changes in the abundance of *Sphagnum* moss at the site. Instead, *Sphagnum* spore frequencies likely reflect changes in sporophyte production and spore release through time with peaks corresponding with environmental conditions that were ideal for sexual reproduction. Water table depth is a major determinant of reproductive mode, and even if sporophytes are produced, sexual reproduction may be unsuccessful if sporophytes are inundated or desiccate before maturation, both of which limit spore production and dispersal (Sundberg, 2002). It is also possible that temporal variability in the frequency of *Sphagnum* spores reflects changes in the abundance of different *Sphagnum* species with disparate spore production and/or changes in the microtopography of the bog surface, as hummocks and hollows typically host different *Sphagnum* species (Sundberg, 2002).

Procrustes analysis demonstrates that the pollen and NPP datasets share similar overall structure with biostratigraphic changes that are comparable in timing and magnitude. The significant congruence (r=0.637, P<0.0001) is noteworthy given that the two proxy records provide information about different aspects of environmental change at different spatial scales: the pollen assemblages primarily reveal regional vegetation dynamics, whereas the NPP data provide a record of local bog development and changing edaphic and hydrological conditions. The congruence of the pollen and NPP datasets suggests the importance of macroscale climate as a shared long-term driver of change in regional forest composition and local bog development. However, relatively high residuals in the Procrustes analysis, which indicate dissimilarity between the two proxies, occur between 5600 and 7500 cal yr BP and underscore the importance of local-scale factors in peatland dynamics. During this interval, increases in *Amphitrema flavum* and *Assulina muscorum* testate amoebae reflect local changes in hydrological conditions, whereas pollen assemblages show relatively stable regional forest composition through much of the Holocene.

Long-term C and N accumulation

The mean C accumulation rate at PMB (16.1 g/m^2/cal yr) is almost double that of the only other Holocene C accumulation record available from coastal BC: at a slope bog on BC's north coast (Turunen and Turunen, 2003), the long-term rate of C accumulation is only 8.6 g/m^2/cal yr (as reported by Loisel et al., 2014). At peatlands further north along the coast in southern Alaska, mean C accumulation is similar to these two records with rates between 8.9 and 18.2 g/m^2/cal yr (Jones and Yu, 2010; Nichols et al., 2014; Loisel et al., 2014). C accumulation at these oceanic sites in the northeast Pacific is lower than Loisel et al.'s (2014) estimate for northern peatlands (22.9 g/m^2/cal yr) and significantly lower than rates in continental fens in western Canada (32.5 g/m^2/cal yr; Yu et al., 2014) and in peatlands on the Tibetan Plateau (31.1 g/m^2/cal yr; Zhao et al., 2014). Continental peatlands tend to accumulate more C on average than oceanic bogs for a number of reasons: higher bulk density of peat, greater seasonality in temperature which promotes primary production in the summer and reduces decomposition in the winter, and lower likelihood of drought if groundwater sources are present (Asada and Warner, 2005; Yu et al., 2014). Although oceanic bogs tend to have higher net primary production than continental peatlands, likely due to a protracted growing season and abundant precipitation, this is accompanied by higher decomposition that acts as a counterbalance, leading to lower overall peat accumulation and C sequestration (Malmer and Wallén, 1993; Asada and Warner, 2005). Gorham et al. (2003) found a strong negative correlation ($r = -0.76$, $P<0.05$) between mean annual precipitation and long-term rates of peat accumulation in North American peatlands (n=21 peat cores), but their study did not include sites with 1400-2900 mm/yr of precipitation. Port McNeil Bog with 1900 mm/yr and a long-term peat accumulation rate of 29.3 g/m^2/cal yr helps to fill that sampling gap. Our results from northern Vancouver Island are in line with Gorham et al.'s (2003) predicted negative relationship between precipitation and peat accumulation, lending further support to the notion that long-term rates of peat accumulation are inversely related to precipitation.

Although C accumulation at PMB and other sites in the northeast Pacific are, on average, lower than in continental settings, the temporal trend in C accumulation over the Holocene is similar to that at many peatlands in the Northern Hemisphere (Yu et al., 2009; Loisel et al., 2014). At

PMB, C accumulation is highest (~31 g/m^2/cal yr) during the earliest Holocene, when temperatures were higher, precipitation was lower, and the seasonal cycle of insolation was amplified relative to the present (Figure 7). As in many northern peatlands (Loisel et al., 2014), maximum C accumulation rates coincide with the timing of the Holocene thermal maximum. Yu et al. (2014) point out that greater seasonality in the early Holocene (i.e., low winter insolation and high summer insolation) would have favoured primary production in summer and reduced decomposition during winter, leading to high C accumulation. Through the mid- to late Holocene, when climate was generally cooler, wetter and less seasonal than in the early Holocene (Figure 7), C accumulation at PMB is markedly lower (14 g/m^2/cal yr, on average), as it is in most northern peatlands.

N accumulation in peatlands has received far less attention and there is a paucity of studies on N accumulation in Pacific North America peatlands to compare to our record from northern Vancouver Island. At PMB, the time-weighted mean NAR is 0.4 g/m^2/cal yr and this compares well with Loisel et al.'s (2014) estimate of 0.5 g/m^2/cal yr for northern peatlands over the Holocene. Overall N accumulation at PMB follows C accumulation, as would be expected given that both are calculated using the same bulk density measurements and accumulation rates and both are related to primary productivity and decomposition. N accumulation is relatively high (~1.2 g/m^2/cal yr) in the warm and drier early Holocene and low (~0.2 g/m^2/cal yr) after 7500 cal yr BP under cooler, wetter and less seasonal climate. The correlation between Holocene changes in climate, in particular seasonality, and C and N accumulation underscores the importance of macroscale climate as a dominant control on long-term C and N accumulation in peatlands.

Although Holocene trends in C and N accumulation follow long-term changes in climate, changes in plant functional groups and local hydrological conditions also play an important role in driving fluctuations in accumulation rates. At PMB, C and N accumulation are high during accumulation of early Holocene herbaceous peat, when C:N ratios are relatively low and multiple proxies suggest the presence of standing water and/or bog pools. Despite lower precipitation, wet conditions at PMB would have lowered overall decay and facilitated higher rates of C and N accumulation in the early Holocene. C and N accumulation decrease abruptly at ~8000 cal yr BP, when the water table lowered relative to the surface and the site became a *Sphagnum* bog. By about 5000 cal yr BP, C and N accumulation show notable increases with further lowering of the water table, the transition to an Ericaceae-dominated bog, and the associated accumulation of ligneous peat. The decrease in C accumulation at PMB between ~3000 and 1000 cal yr BP coincides generally with Neoglacial cooling and glacial advances in the adjacent Coast Mountains of BC (e.g., Coulthard et al., 2013), but also to an interval of high charcoal concentrations (Figure 3). It is likely that disturbance from fire removed some portion of the bog's surface vegetation and enhanced decomposition. Slower net peat addition during this time likely reflects an increase in decomposition rather than a substantial decrease in productivity.

Conclusion

In the warm, relatively dry early Holocene, Port McNeill Bog was a herb-dominated peatland with *Nuphar* in standing water and/or bog pools, set within mixed coniferous forest with scattered *Pseudotsuga menziesii*. C and N accumulation were highest during this interval with mean rates of 30.6 g/m^2/cal yr and 1.2 g/m^2/cal yr, respectively. By about 8000 cal yr BP, regional forests transitioned under a cooler, wetter climate to *Tsuga heterophylla*-dominated rainforests, similar to those that still occupy the region today. On a local scale, lowering of relative water table depth facilitated the development of a *Sphagnum* bog by 8000 cal yr BP, with an increasing abundance of ericaceous shrubs and further lowering of the water table after 5000 cal yr BP. C and N accumulation rates were low during accumulation of *Sphagnum* peat, particularly between ~7000 and 5500 cal yr BP, and then increased during accumulation of ligneous peat in the mid- to late Holocene. Temporal changes in the frequency and concentration of *Sphagnum* spores do not correlate well with stratigraphic changes in *Sphagnum* macro-remains or peat type, suggesting that *Sphagnum* spore records may not always reflect the abundance of *Sphagnum* moss accurately.

This is the first multi-proxy peat study in coastal BC that spans the full Holocene and our results underscore the importance of using a multi-proxy approach in peat-based paleoenvironmental studies. Procrustes analysis is an effective numerical tool for revealing similarities and differences in proxy records; however, physicochemical records are essential for a more complete understanding of bog development and peat C and N accumulation. Our study shows that changes in plant functional groups, local hydrological conditions, and macroscale climate interact to affect C and N accumulation in bog ecosystems on long ecological timescales. Peat C accumulation on northern Vancouver Island was significantly higher during the early Holocene, but the overall rate of accumulation is significantly lower than in continental peatlands. This suggests that differences in seasonality play an important role in driving C accumulation, both on long temporal scales and at large spatial scales. Additional research is needed from other sites on the northeast Pacific coast in order to better understand how long-term changes in climate, vegetation and hydrology have shaped peatland development and C and N accumulation in this oceanic setting.

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Table 1. AMS radiocarbon and calibrated calendar ages on wood from Port McNeill Bog, Vancouver Island, British Columbia.

Depth (cm)	Radiocarbon Age (^{14}C yr BP ± 1σ)	δ^{13}C (‰)	Calendar Age (cal yr BP)[a]	Lab No.
30-31	740 ± 30	–24.8	683 (660-730)	Beta-365555
65-66	2850 ± 30	–28.8	2961 (2880-3060)	Beta-337811
109-110	4110 ± 30	–25.9	4654 (4520-4810)	Beta-337812
124-125	4690 ± 30	–24.2	5412 (5320-5580)	Beta-365556
140-141	6240 ± 40	–24.4	7157 (7010-7260)	Beta-335265
234-235	8160 ± 40	–24.5	9109 (9010-9250)	Bets-335266
321-322	9220 ± 40	–23.9	10,380 (10,260-10,500)	Beta-335267

[a] Weighted average of the probability distribution and 2σ age range rounded to the nearest 10 yr.

Figure Captions

Figure 1. Location of Port McNeill Bog (PMB) on northern Vancouver Island, British Columbia, Canada and other sites mentioned in the text: 1. Tiny Lake (Galloway et al., 2009), 2. Two Frog Lake (Galloway et al., 2007), 3. Woods Lake (Stolze et al., 2007), 4. Cook Bank (Lacourse et al., 2003), 5. Bear Cove Bog (Hebda, 1983), 6. Misty Lake (Lacourse, 2005), 7. Pyrola Lake (Hebda and Haggarty, 1997), and 8. Kalmia Lake (Hebda and Haggarty, 1997).

Figure 2. Age-depth model for the Port McNeill Bog core with 95% confidence intervals shown as grey bands. The model is based on a Stineman interpolation fit using ‘stinepack’ (Johannesson and Bjornsson, 2012) and ‘clam’ (Blauuw, 2010).

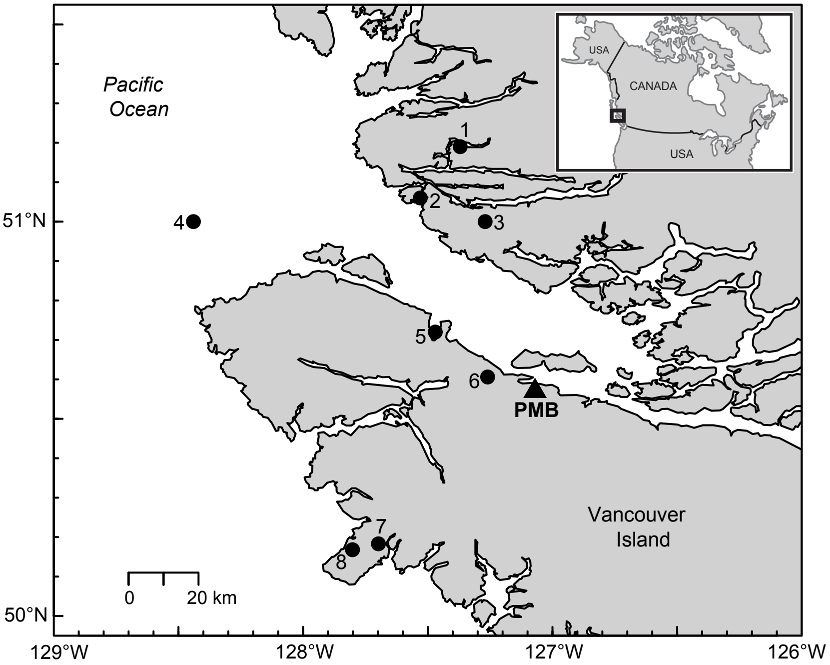
Figure 3. Peat stratigraphy, peat component percentages and plant macrofossils for Port McNeill Bog, northern Vancouver Island. UOM= unidentifiable organic matter.

Figure 4. Pollen and spore percentages for Port McNeill Bog, northern Vancouver Island showing major taxa only and 10× exaggeration of infrequent taxa. Circles within the plot of *Sphagnum* spores denote the stratigraphic position of spores of the parasitic fungus, *Tilletia sphagni* (NPP Type 27).

Figure 5. Concentrations of major non-pollen palynomorphs for Port McNeill Bog. Note changes in scale on the x-axes. *Hyalosphenia subflava* reaches a maximum of 162,000/cm^3 (off scale) at ~400 cal yr BP. Circles within the plot of *Assulina muscorum* denote the stratigraphic position of *A. seminulum* tests. Numbers in brackets refer to Pals et al. (1980) NPP types.

Figure 6. Peat stratigraphy and physicochemical records from Peat McNeill Bog, northern Vancouver Island. See Fig. 3 for peat stratigraphy legend. LOI=loss on ignition.

Figure 7. Summary peat composition, C:N ratios, and carbon (CAR) and nitrogen (NAR) accumulation rates at Port McNeill Bog, Vancouver Island. Relatively wet conditions are inferred from herbaceous, brown moss and unidentifiable organic material percentages and relatively dry conditions from *Sphagnum* and Ericaceae percentages, following Loisel and Yu (2013). Also shown are pollen-inferred mean annual precipitation (MAP) for southwest British Columbia (Mathewes and Heusser, 1981), C_{37} alkenone-inferred sea surface temperature (SST) from immediately west of Vancouver Island (Kienast and McKay, 2001), and January and July insolation anomaly at 50°N (Berger and Loutre, 1991).



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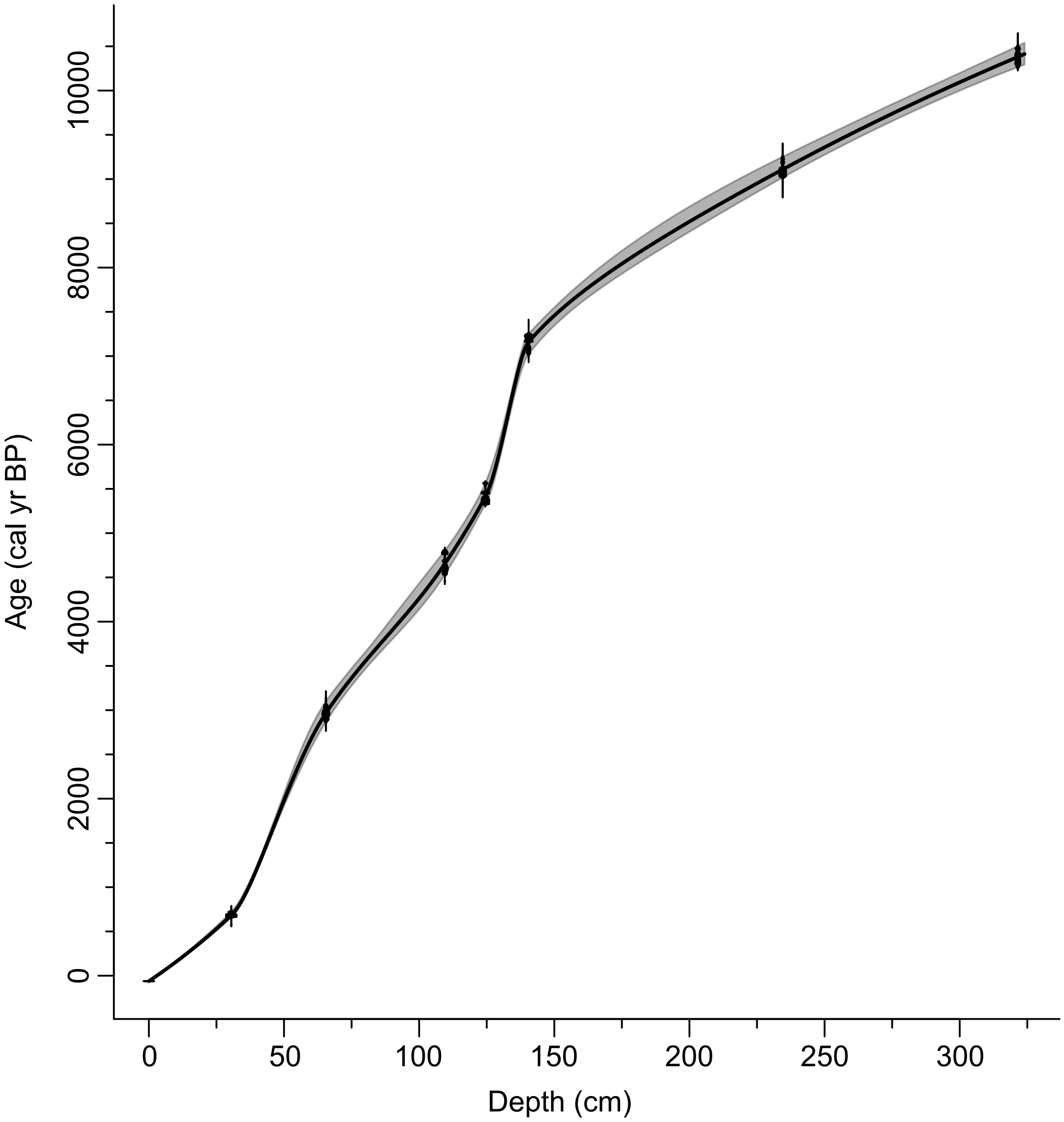

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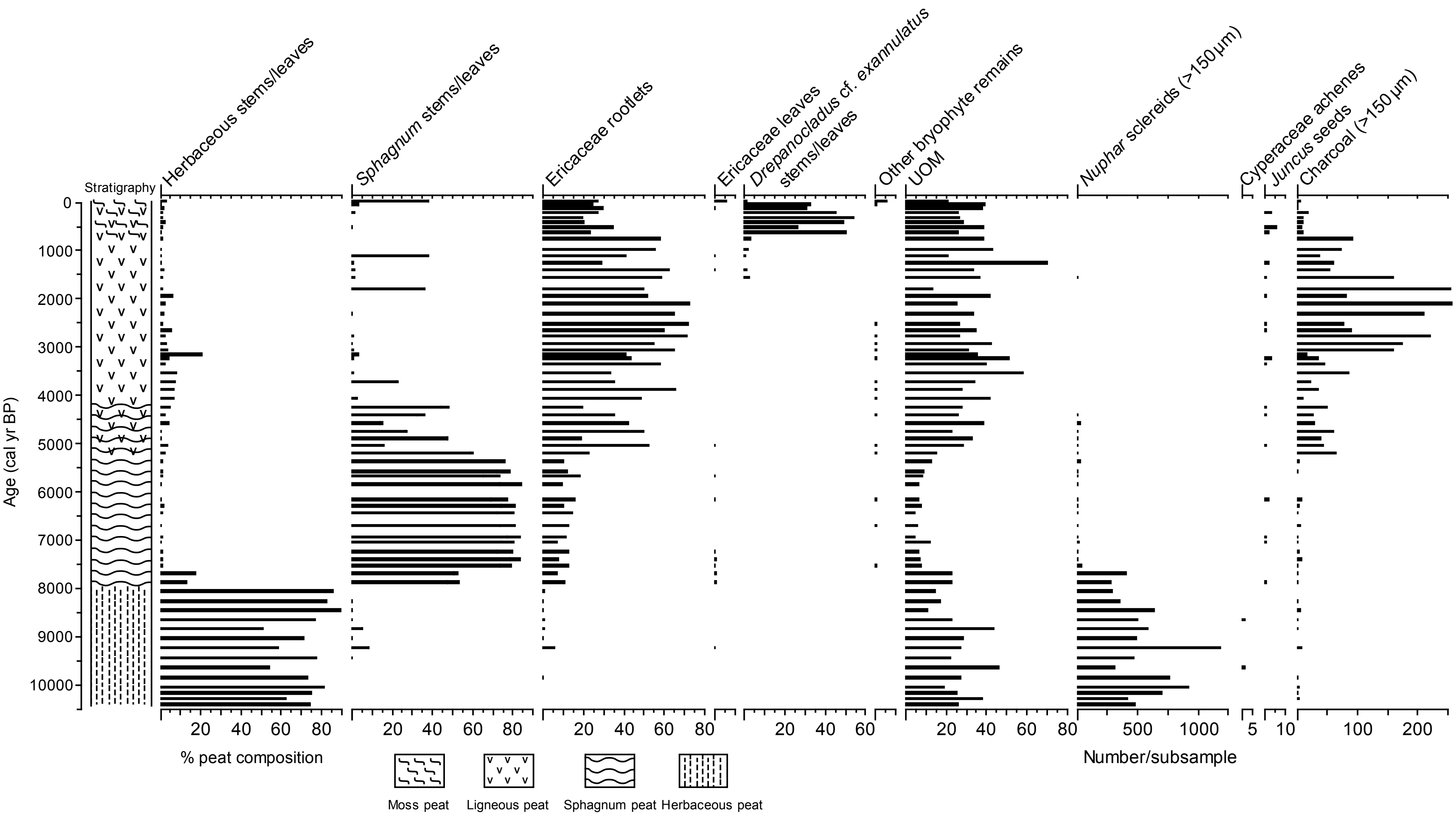

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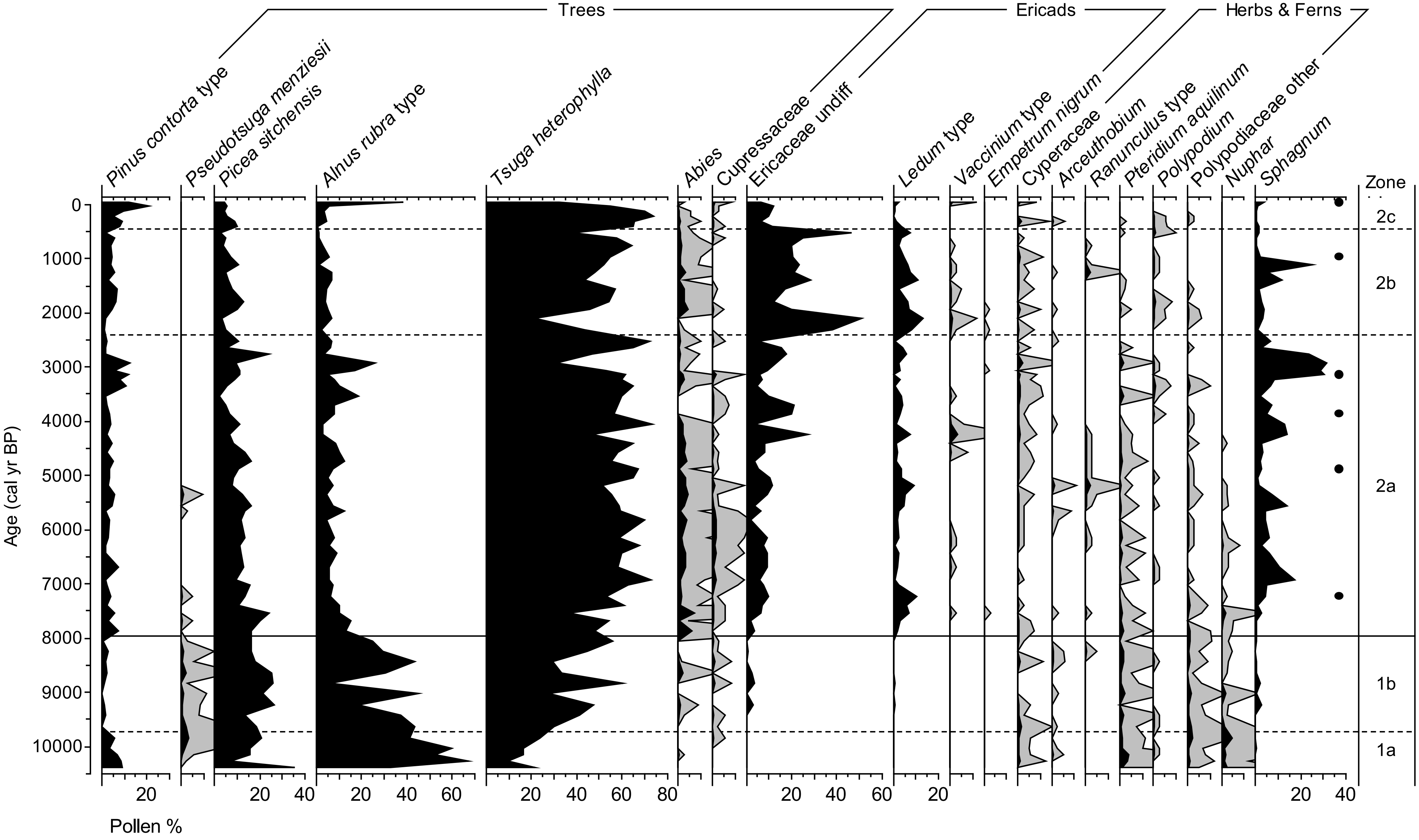

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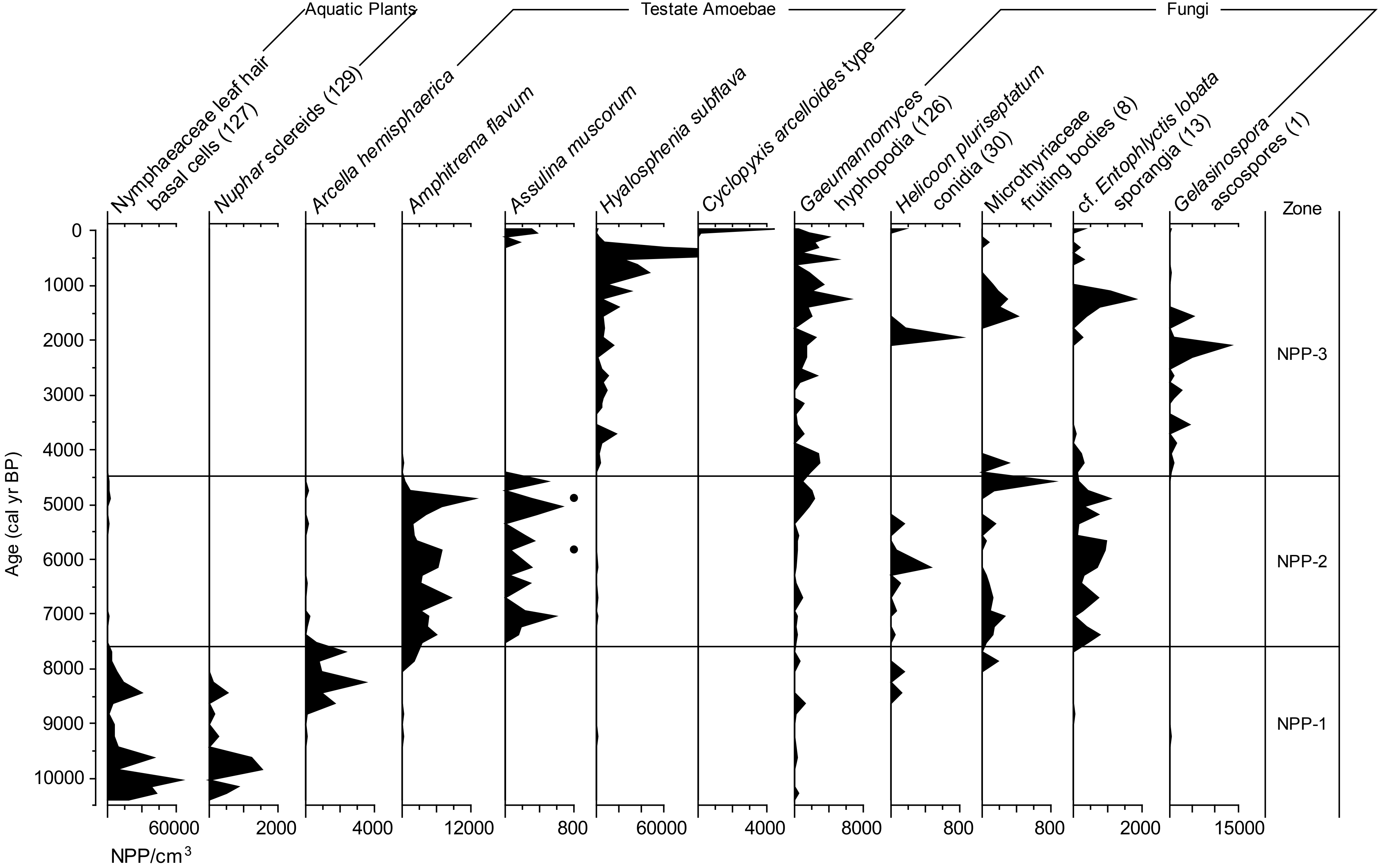

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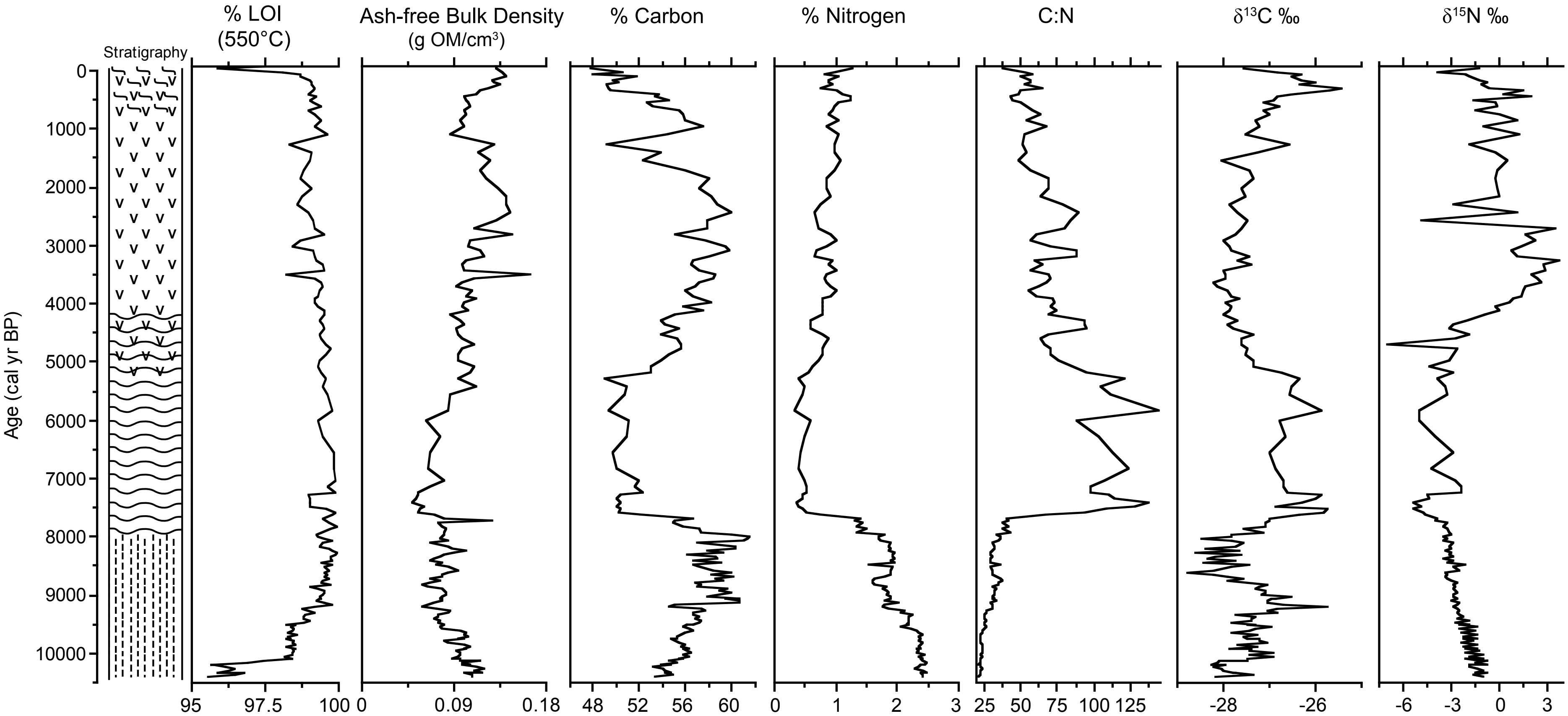

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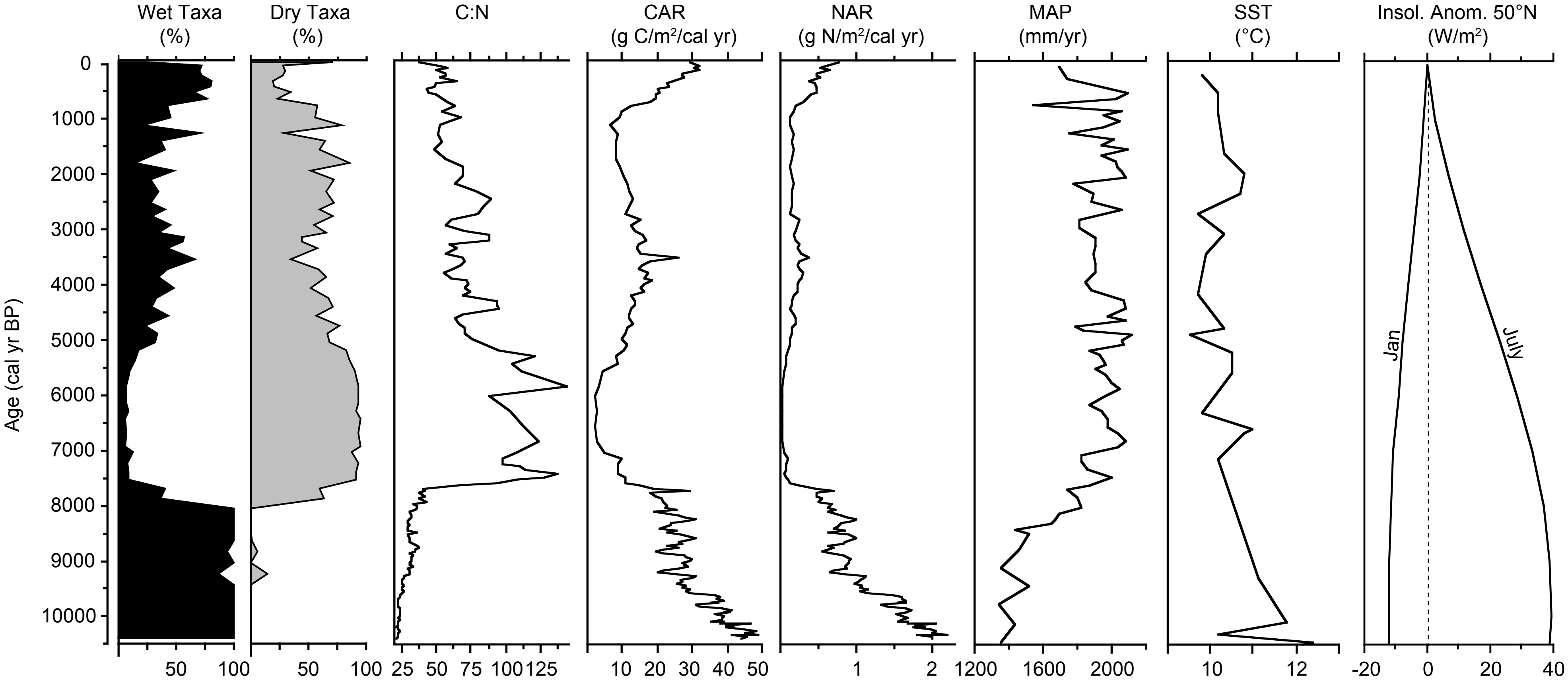

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