https://doi.org/10.5194/cp-2020-32
Preprint. Discussion started: 24 March 2020

Climate of the Past Discussions

Paleobotanical proxies for early Eocene climates and ecosystems in northern North America from mid to high latitudes

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Abstract. Early Eocene climates were globally warm, with ice-free conditions at both poles. Early Eocene polar landmasses supported extensive forest ecosystems of a primarily temperate biota, but also with abundant thermophilic elements such as crocodilians, and mesothermic taxodioid conifers and angiosperms. The globally warm early Eocene was punctuated by geologically brief hyperthermals such as the Paleocene-Eocene Thermal Maximum (PETM), culminating in the Early Eocene Climatic Optimum (EECO), during which the range of thermophilic plants such as palms extended into the Arctic. Climate models have struggled to reproduce early Eocene Arctic warm winters and high precipitation, with models invoking a variety of mechanisms, from atmospheric CO_2 levels that are unsupported by proxy evidence, to the role of an enhanced hydrological cycle to reproduce winters that experienced no direct solar energy input yet remained wet and above freezing. Here, we provide new estimates of climate, and compile existing paleobotanical proxy data for upland and lowland mid-latitudes sites in British Columbia, Canada, and northern Washington, USA, and from high-latitude lowland sites in Alaska and the Canadian Arctic to compare climatic regimes between mid- and high latitudes of the early Eocene—spanning the PETM to the EECO—of the northern half of North America. In addition, these data are used to reevaluate the latitudinal temperate gradient in North America during the early Eocene, and to provide refined biome interpretations of these ancient forests based on climate and physiognomic data.

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1 Introduction

The early Eocene (56–47.8 million years ago) was a globally warm interval in Earth history, which resulted from a warming trend that began in the late Paleocene (Zachos et al., 2008; Carmichael et al., 2016). This warming was punctuated by a series of episodic hyperthermal events (e.g., the Paleocene-Eocene Themal Maximum and the Eocene Thermal Maximum 2), which caused global climatic perturbations, and ultimately culminated in the early Eocene Climatic Optimum (EECO) (Zachos et al., 2008; Littler et al., 2014; Laurentano et al., 2015; Westerhold et al., 2018). During the early Eocene, the climate of much of northern North America was warm and wet, with mean annual temperatures (MAT) as high as 20 °C, mean annual precipitation (MAP) of 100–150 cm a^{-1}, mild frost-free winters (coldest month mean temperature >5 °C), and climatic conditions that supported extensive temperate forest ecosystems (e.g., Wing and Greenwood, 1993; Wing, 1998; Shellito and Sloan, 2006; Smith et al., 2012; Breedlovestrout et al., 2013; Herold et al., 2014; Greenwood et al., 2016).

These warm and wet conditions extended poleward in North America, despite extreme photoperiodism, promoting the establishment of temperate forest ecosystems and thermophilic biota (e.g., mangroves, palm trees, and alligators) (Eldrett et al., 2009, 2014; Sluijs et al., 2009; Huber and Caballero 2011; Eberle and Greenwood, 2012; Littler et al., 2014; West et al., 2015, 2019; Salpin et al., 2019), and providing evidence for a shallow latitudinal temperature gradient, in contrast to the much higher gradient of modern North America (Greenwood and Wing, 1995; Naafs et al., 2018). The reconstructed paleoclimatic and biotic similarity between the mid- and high latitudes of Eocene North America may be counterintuitive given the limited photic seasonality of mid-latitude sites and the extreme seasonal photic regime of high-latitude environments. In spite of similar thermal regimes, one would expect that the Arctic ecosystems would have experienced unparalleled abiotic stress from the extended period of winter darkness (West et al., 2015), and, as a result, would have had a substantially different climate and biota from that of contemporaneous mid-latitudes sites. Fossil evidence from both the mid- and high latitudes, however, demonstrate little to no discernable effect.

Fossil plants are among the best proxies for terrestrial paleoclimates, as plants are sessile organisms that interact directly with their environment, and whose phenotype is highly moderated by variables such as temperature, moisture, and atmospheric carbon availability. Despite this, paleobotanical proxy reconstructions of temperature and precipitation are often mismatched with General Circulation Model (GCM) simulation output, and, models struggle to reproduce the warm high-latitude regions and reduced latitudinal temperature gradient of the early Eocene as evidenced from the fossil record (Huber and Caballero, 2011; Huber and Goldner, 2012; Herold et al., 2014; Carmichael et al., 2016; Lunt et al., 2017, 2020; Keery et al., 2018; Naafs et al., 2018; Hollis et al., 2019). This suggests that some atmospheric processes related to heat transfer may be missing from GCM simulations (Carmichael et al., 2018, and references cited therein). Furthermore, there are far fewer compilations of terrestrial temperature proxy data as compared to marine-based data compilations of sea surface temperatures (SST) (Hollis et al., 2019). This results in spatial, or

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geographic, gaps in proxy data—essentially the paucity of data requires that proxy climate data separated by considerable distance must be used to interpolate climate over large geographic areas—that impede the efficacy of GCM simulations (Hollis et al., 2019). However, concerted efforts have been made to fill the geographic gaps through the development of new, targeted compilations and additional proxy data (e.g., DeepMIP, Hollis et al., 2019; Lunt et al., 2020). In addition, models do not typically incorporate potential vegetative feedbacks (Lunt et al., 2012), although advances in defining functional plant types have been made (Loptson et al., 2014).

Therefore, there is a need to refine the quality and consistency of physiognomic and Nearest Living Relative (NLR) paleobotanical proxy data estimates, provide new physiognomic and NLR proxy data to help fill regional and temporal gaps, and provide more reliable forest biome interpretations. An emphasis needs to be placed on multi-proxy studies that evaluate an ensemble of proxy estimates, which allows for identifying strongly congruent paleoclimate proxy reconstructions where the results agree, and inconsistencies where the failures of individual proxy estimates can be identified. Thus, the purpose of this study is to reconsider reported, and introduce new, early Eocene paleobotanical climate data from northern North America utilizing a refined methodology where a bootstrapping approach is applied to the data to produce ensemble climate estimates. Paleobotanical-based paleoclimate reconstructions from northern North America are reviewed, and new paleoclimate estimates are provided for British Columbia and the Canadian Arctic through application of a multi-proxy ensemble approach, as recommended by Hollis et al. (2019) and others (e.g., Reichgelt et al., 2018, Lowe et al., 2018; Willard et al., 2019) in order to mitigate potential errors resulting from variations between methods.

Paleobotanical assemblages from four distinct regions in northern North America are considered here: mid-latitude lowland sites; mid-latitude upland sites; low polar lowland sites; and high polar lowland sites. Comparison of lowland sites allows for reevaluation of the terrestrial latitudinal temperature gradient in northern North America. Furthermore, the distribution of vegetation, as potentially moderated by climate, elevation, continentality, and photoperiod is evaluated through comparisons of the mid-latitude upland and high-latitude lowland fossil localities. This is achieved by plotting climate data on biome diagrams, as well as principal component analysis (PCA) and hierarchical cluster analysis (HCA) of leaf physiognomy. This provides a more robust interpretation of these ancient forested ecosystems, which will contribute to refinement of modelling simulations by providing reliable insight for prescribing early Eocene boundary conditions for high latitude vegetation and environments.

2 Materials and Methods

2.1 Fossil plant localities

Early Eocene paleobotanical proxy data are sourced from multiple fossil localities from the northern mid-latitudes (48.3–51.2 °N) and high latitudes (61.4–81.4 °N) of North America, primarily within Canada, but also including sites from Washington State and Alaska (Table 1). In

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general, the majority of fossil localities used for this study were within a few degrees latitude of their present position, as North America has moved obliquely past the rotational pole since the Eocene. As the resulting slight poleward displacement is not significant for the present work, we report modern latitudes for the compilation of fossil localities within this study to avoid discrepancies in differing methods of estimating paleolatitudes. These localities represent both lowland and upland ecosystems. Prior physiognomic analyses of fossil megaflora from both the mid-latitudes and high-latitudes of North America indicate that these ancient forests were growing under similar thermal regimes (e.g., MAT 10–15 °C and MAP 100–150 cm a^{-1}) (Wing and Greenwood, 1993; Greenwood and Wing 1995; Smith et al. 2012; West et al., 2015; Gushulak et al., 2016; Greenwood et al., 2016; Lowe et al., 2018). The Canadian fossil localities (e.g., British Columbia and Nunavut) are stratigraphically correlated, placing all the fossil study sites into a chronological sequence spanning the early Eocene (McIver and Basinger 1999; Greenwood et al., 2016; Eberle and Greenwood 2017; West et al., 2019). Other localities within our data set (e.g., Evan Jones Mine, AK, Racehorse Creek, and Republic, WA) are also considered equivalent in age, and the stratigraphic relationships for these floras may be found in the respective publications for these localities (Table 1).

2.1.2 Mid-latitude Upland Fossil Plant Localities

The Okanagan Highlands host a suite of mid-latitude upland fossil floras from British Columbia and Washington (Archibald et al., 2011; Greenwood et al., 2016) (Table 1, Fig. 1). These fossil localities have been dated radiometrically as early Eocene, likely occurring within the EECO (Moss et al., 2005; Smith et al., 2009; Greenwood et al., 2016; Mathewes et al., 2016; Lowe et al., 2018). Okanagan Highland floras are broadly similar in floristic composition, comprised of a high diversity of plant genera typical of modern temperate deciduous and subtropical evergreen forests (DeVore and Pigg, 2010; Smith et al., 2012; Gushulak et al., 2016; Lowe et al., 2018). These forests were regionally extensive, occupying north-south orientated and arc-related volcanic highlands (Mathewes 1991; Lowe et al., 2018). The paleoelevation of these sites has been reconstructed to be between 500–1500 m based on both paleobotanical and geochemical proxies (Wolfe et al., 1998; Greenwood et al., 2005, 2016; Tribe, 2005; Smith et al., 2012), and as a result of this altitude, these forests would have experienced cooler temperatures than the coastal lowlands to the west (Wolfe et al., 1998; Greenwood et al., 2016; Lowe et al., 2018). In addition to plants, fossil insect diversity is high, similar to modern day tropical forests (Archibald et al., 2010, 2013)

2.1.3 Mid-latitude Lowland Fossil Plant Localities

The uppermost Paleocene to middle Eocene Chuckanut Formation of western Washington State (Fig. 1) contains several fossil floras representing subtropical coastal lowland ecosystems, including palms and many other thermophilic plant taxa (Breedlovestrout et al., 2013; Mathewes et al., 2020). The Chuckanut floras used for this study are the Racehorse Creek fossil localities, which are found within the Slide Member (Fig. 2), a thick terrestrial deposit that has been radiometrically dated to the early Eocene (Breedlovestrout et al. 2013).

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2.1.4 High-latitude Low Polar Lowland Fossil Localities

The Chickaloon Formation in south-central Alaska (Fig. 1) preserves a fossil flora known from the Evan Jones Mine (Sunderlin et al., 2011), herein referred to as the Evan Jones Mine flora. Wolfe et al., (1966) assigned a Paleocene age to the Chickaloon Formation based on K-Ar dating. However, fission-track zircon dating shows that the Paleocene-Eocene boundary occurs within the upper 150 m of the Chickaloon Formation (Triplehorn et al., 1984), stratigraphically near the fossil flora (Fig. 2) and therefore the Chickaloon Formation straddles the Paleocene-Eocene boundary (*sensu* Sunderlin et al., 2011). The Evan Jones Mine flora represents a lowland warm temperate to subtropical floodplain forest, as fossil palms are present and a high proportion of the flora exhibits leaves with untoothed margins (Wolfe et al., 1966; Sunderlin et al., 2011).

2.1.3.5 High-latitude High Polar Lowland Fossil Localities

Fossil floras from Ellesmere and Axel Heiberg islands in Nunavut, Canada, are the most northerly fossil sites included in this study (Fig. 1). These fossil floras have been sampled extensively from formations within the Eureka Sound Group, primarily from the Mount Lawson, Mount Moore, and Margaret (=Iceberg Bay) formations (Fig. 2) (McIver and Basinger, 1999; West et al., 2019). The Margaret Formation at Stenkul Fiord and the Mount Lawson Formation at Split Lake have been radiometrically dated to the early Eocene (Reinhardt et al., 2013, 2017). Additional age controls (i.e. vertebrate fossils, palynology, paleomagnetic dating) suggest either late Paleocene, early Eocene, or both for all three formations at various localities (Eberle and Greenwood, 2012; West et al., 2019). The fossil floras of the Canadian Arctic are therefore considered to represent the late Paleocene to early Eocene time interval, with some localities capturing the PETM and ETM-2 hyperthermal events (e.g., Stenkul Fiord) (Sudermann et al., in review). These high-latitude fossil floras represent lowland environments and are considered warm temperate floodplain or swamp forests (McIver and Basinger, 1999; Greenwood et al., 2010; West et al., 2019). Although this high-Arctic assemblage as a whole is of a high taxonomic richness (see West et al., 2019), the site-to-site diversity (β diversity) is the lowest within the compilation for this study.

2.2 Sampling

At the majority of the fossil sites from British Columbia, fossil leaves were comprehensively sampled along bedding planes, using census sampling (i.e. collecting >300 leaf morphotype specimens; Wilf, 2000; Lowe et al., 2018). Some sites, such as those from the Canadian Arctic (i.e., Ellesmere and Axel Heiberg islands) and others from British Columbia (i.e., Chu Chua, Driftwood Canyon, One Mile Creek, Thomas Ranch), represent leaf collections from prior work by earlier researchers where sampling was selective to yield a representative sample of the leaf taxa present. Some localities reported in this study were not sampled by the authors (e.g., Evan Jones Mine, Alaska; Chu Chua, One Mile Creek, Quilchena and Thomas Ranch, BC; Racehorse Creek and Republic, WA), therefore the details of the sampling protocols for those floras may

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differ from sampling methods outlined above. The sampling methods for those fossil sites can be found in their original respective publications (Table 1).

2.3 Paleoclimate Analyses

2.3.1 Ensemble Climate Analysis

We apply an ensemble climate analysis approach that avoids choosing one method over another, so that we can present the results from each method as well as the consensus reconstruction based on all methods (Greenwood, 2007; Gushulak et al., 2016; Greenwood et al., 2017; Lowe et al., 2018; Willard et al., 2019; Hollis et al., 2019). The ensemble approach also highlights potential disparity between different proxy reconstructions. This approach is applied to both physiognomic and bioclimatic analysis (BA) climate data compilations (see below). Statistically assessed ensemble estimates of Mean Annual Temperature (MAT), Coldest Month Mean Temperature (CMMT), Warmest Month Mean Temperature (WMMT), and Mean Annual Precipitation (MAP) were produced by bootstrapping results of high mid-latitude and high-latitude fossil site physiognomic and BA data. The mean and standard deviations were resampled using n=1000 Monte Carlo simulations for each proxy reconstruction at each site. A probability density function was then calculated for each climatic variable, for each site. The BA-based summer mean temperature (ST) and winter mean temperature (WT) estimates (see section 2.3.3 below for a discussion of these terms) were transformed to WMMT and CMMT, respectively, using a method described in Reichgelt et al. (2018), wherein a linear regression function between ST and WMMT, and WT and CMMT is used to calculate values in NLR that can be directly compared to physiognomic proxy results (Figure A1). This method is in line with the recommendations of Hollis et al. (2019), where a statistically-assessed multi-proxy consensus approach should be utilized when feasible for reconstructing terrestrial climate.

2.3.2 Leaf Physiognomy

Leaf physiognomy methods, such as Climate Leaf Analysis Multivariate Program (CLAMP) and Leaf Area Analysis (LAA), utilize correlations between leaf architecture and climate variables derived from modern global vegetation databases to provide estimates of paleoclimate variables (Greenwood, 2007; Peppe et al., 2011; Yang et al., 2015; Hollis et al., 2019). Hollis et al. (2019) noted the potential for disparity between fossil plant-based climate proxies and calibrations within individual proxies that can contribute to differences in climate estimates, and as such represent a challenge for model-data comparisons for the Eocene.

We primarily report physiognomically derived paleoclimate estimates from CLAMP, as these were readily available from some localities from prior studies (e.g., Wolfe et al., 1998; Sunderlin et al., 2011; Smith et al., 2012; Breedlovestrout et al., 2013; Dillhoff et al., 2013; West et al., 2015; Gushulak et al., 2016; Mathews et al., 2016; Lowe et al., 2018), and because CLAMP provides estimates of seasonal temperatures and precipitation. The use of CLAMP estimates allows comparisons between the paleontological proxy estimates of winter temperatures and the

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seasonality of precipitation with climate model output, parameters that are of interest in understanding early Eocene climates at mid- and high latitudes (Huber and Caballero, 2011; Huber and Goldner, 2012; Carmichael et al., 2016; Hollis et al., 2019). For sites where the original published CLAMP estimates were incomplete or run early in the development of CLAMP (e.g., Chu Chua, One Mile Creek and Republic; Wolfe et al., 1998), we have re-run the CLAMP analyses using the original score sheets archived on the CLAMP online website. The Physg3brcAZ vegetation and the GRIDMet3brcAZ meteorological datasets were used for the analyses run for this study (Yang et al., 2015). For CLAMP estimates sourced from existing studies, the vegetation and meteorological datasets are reported in those sources (Table 1).

The estimates from CLAMP are supplemented with estimates using leaf area analysis (LAA) for mean annual precipitation (Wilf et al., 1998; Peppe et al., 2011) a climate parameter not typically provided by CLAMP, as well as leaf margin analysis (LMA) for mean annual temperature (Wilf, 1997; Greenwood, 2007; Peppe et al., 2011). Estimates for Falkland, Quilchena and Thomas Ranch in British Columbia, Evan Jones Mine in Alaska, and three sites from Ellesmere Island in Nunavut are reported from the original analyses of those localities, but are supplemented with previously unreported CLAMP paleoclimate estimates from some of these localities (Wolfe et al., 1998; Breedlovestrout, 2011; Smith, 2011; Sunderlin et al., 2011; Smith et al., 2012; Breedlovestrout et al., 2013; Dillhoff et al., 2013; West et al., 2015).

2.3.3 Bioclimatic Analysis

In addition to physiognomic analyses, we employ Bioclimatic Analysis (BA) (Greenwood et al., 2005), which extracts paleoclimatic information from fossil assemblages based on the modern-day distribution of nearest living relatives (NLR) of the taxa found in the fossil assemblage. Here, BA was performed by calculating probability density functions (e.g., Greenwood et al., 2017; Hyland et al., 2018; Willard et al., 2019) for each site and each climatic variable: MAT, ST, WT and MAP.

ST and WT represent the average temperature for the three warmest and coldest months, respectively. This is in contrast with WMMT and CMMT output of CLAMP, which represent the mean temperature during the warmest and coldest month, respectively. This is the result of the gridded climate data used in these approaches; BA relies on Hijmans et al. (2005), whereas CLAMP relies on gridded climate data of New et al. (2002). Modern-day plant distributions were derived from the Global Biodiversity Information Facility, which were then cross-plotted with gridded climatic maps using the ‘dismo’ package in R (Hijmans et al., 2005) in order to calculate means (μ) and standard deviation (σ) for each taxon and each climatic variable. The geodetic records were first filtered in order to remove recorded occurrences with uncertain taxonomic assignments, as well as exotic and duplicate occurrences. Additionally, a random subset of the geodetic data was created that filtered out all but three occurrences in every $0.1° \times 0.1°$ gridcell and all but 10 in every $1° \times 1°$ gridcell. This is to avoid overrepresentation of oversampled regions of the world.

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Grimm and Potts (2016) pointed out that assessing the bioclimatic range of plant taxa for each climatic variable separately may create an 'apparent bioclimatic envelope', where none of the occurrences fall within a certain combination of temperature and precipitation, but the climatic combination is still possible due to this apparent overlap. To circumvent this problem, we assess the likelihood (f) of a taxon (t) occurring at a combination of climatic variables, in this case MAT, ST, WT and MAP.

$$f(t_n) = \left(\frac{1}{\sqrt{2\sigma_{MAT}{}^2\pi}} e^{(x_{MAT}-\mu_{MAT})^2/2\sigma_{MAT}{}^2}\right) \times \left(\frac{1}{\sqrt{2\sigma_{ST}{}^2\pi}} e^{(x_{ST}-\mu_{ST})^2/2\sigma_{ST}{}^2}\right) \times \left(\frac{1}{\sqrt{2\sigma_{WT}{}^2\pi}} e^{(x_{WT}-\mu_{WT})^2/2\sigma_{WT}{}^2}\right) \times \left(\frac{1}{\sqrt{2\sigma_{MAP}{}^2\pi}} e^{(x_{MAP}-\mu_{MAP})^2/2\sigma_{MAP}{}^2}\right) \quad (1)$$

Any combination of climatic variables can be assessed in this way. The likelihood of each taxon is then combined to create an overall probability density function (z) for each climatic variable representative of the most likely bioclimatic range of the taxa in the assemblage.

$$f(z) = f(t_1) \times f(t_2) \times \ldots \times f(t_n) \quad (2)$$

This method creates highly variable probability densities, dependent on both the number of taxa and the disparity of the climatic range of the NLR's. The climatic values reported here represent the value with the highest absolute probability, and the 95% Confidence Interval represents the minimum and maximum values at which the absolute probability was ≥5% the maximum probability.

2.4 Biome and Physiognomic Character Analysis

The physiognomic, BA, and ensemble climate estimates of each fossil locality were plotted on a Whittaker (1975) biome diagram, modified from Woodward et al. (2004), in order to determine the corresponding modern biome classification for each paleoforest based on paleoclimatic estimates. In addition, the CLAMP derived physiognomic data of each fossil locality were analyzed using principal component analysis (PCA) against a comprehensive global compilation of modern physiognomic data (Yang et al., 2015; Hinojosa et al., 2011; Reichgelt et al., 2019) to determine the most similar modern physiognomic analogues of the fossil sites. Finally, the physiognomic characteristics of fossil, and a subset of modern, sites were compared using a hierarchical cluster analysis to determine similarity. This was achieved by calculating a Euclidean dissimilarity matrix without scaling using the "cluster" package in R (Maechler et al. 2019) and the "Ward D2" method for Hierarchical Clustering (R Core Team, 2019).

3 Results

3.1 Quantitative paleoclimate analysis from paleobotanical proxies

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3.1.1 Mid-latitude Upland Fossil Plant Localities

Ensemble estimates of MAT for the mid-latitude upland fossil localities of British Columbia and Washington ranged between 7.0–14.9 °C, with the range of mean temperatures for the coldest (CMMT) and warmest months (WMMT) between -0.3–4.3 °C and 18.6–22.7 °C, respectively (Table 2). Ensemble MAP estimates for these localities ranged between 80–135 cm a^{-1} (Table 2), while CLAMP estimates for the three wettest and three driest months (3WET and 3DRY) for these localities ranged between 40.0–66.1 cm (error ± 23 cm) and 11.5–28.9 cm (error ± 6 cm), respectively (Table A1). The complete compilation of site-specific physiognomic and BA data for mid-latitude upland fossils sites of British Columbia and Washington is provided in tables A1–A3.

3.2.2 Mid-latitude Lowland Fossil Plant Locality

Ensemble estimates of MAT for the mid-latitude lowland Racehorse Creek fossil sites from western Washington ranged between 17.3–18.9 °C, with the mean temperatures for the coldest (CMMT) and warmest months (WMMT) between 7.3–11.4 °C and 23.1–23.6 °C, respectively (Table 2). The ensemble MAP estimate for Racehorse Creek was 135 cm a^{-1} (Table 2), while CLAMP estimates for the three wettest and three driest months (3WET and 3DRY) for this locality were 58.7 cm (error ± 23 cm) and a range of 23.4–25.9 cm (error ± 6 cm), respectively (Table A1). The complete compilation of site-specific physiognomic and BA data for Racehorse Creek is provided in tables A1–A3.

3.1.3 High-latitude Low Polar Lowland Fossil Locality

Ensemble estimate of MAT for the Chickaloon Formation Evan Jones Mine fossil flora was 13.7 °C, with estimates of CMMT and WMMT of 6.4 °C and 21.8 °C, respectively (Table 2). The ensemble MAP estimate for the Evan Jones Mine flora was 132 cm a^{-1} (Table 2), while reported CLAMP estimates for the three wettest and three driest months (3WET and 3DRY) from Sunderlin et al. (2011) for this locality were 63.5 cm (error ± 23 cm) and 36.6 cm (error ± 6 cm), respectively (Table A1). The complete compilation of site-specific physiognomic and BA data of the Evans Jones Mine flora from Alaska is provided in tables A1–A3.

3.1.4 High-latitude High Polar Lowland Fossil Localities

Ensemble estimates of MAT for the high-latitude fossil localities from Arctic Canada ranged from 7.6–12.9 °C, with the range of CMMT and WMMT from 1.3–4.2 °C and 18.2–22.2 °C, respectively (Table 2). Ensemble MAP estimates for Ellesmere and Axel Heiberg islands ranged between 131–180 cm a^{-1} (Table 2), while CLAMP estimates for the three wettest and three driest months (3WET and 3DRY) for the Arctic Canada fossil localities ranged between 36.9–54.4 cm (error ± 23 cm) and 19.7–31.3cm (error ± 6 cm), respectively (Table A1). The complete compilation of site-specific physiognomic and BA data for Ellesmere and Axel Heiberg islands fossil plant localities is provided in tables A1–A3. In addition, climate estimates for Lake Hazen

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are produced using BA (Table A3), as taxonomic data for this site recently became available (West et al., 2019). Lake Hazen represents the most northerly (~81 °N) terrestrial plant fossil sites available in North America and as such, climate data from this site help fill important geographic gaps. Although, the number of broadleaf taxa identified at this locality (n = 11) was comparable to other Ellesmere Island fossil localities (e.g., Split Lake), many specimens were fragmentary and incomplete. This limited the number of taxa that could be reliably scored to an insufficient number (n = 6) to run leaf physiognomic analyses with meaningful precision and accuracy (Greenwood, 2007; Peppe et al., 2011; Yang et al., 2015), and as such this site could not be included in the site-specific ensemble analysis.

3.2 Biome types, Principal Component Analysis (PCA), and Hierarchical Cluster Analysis (HCA) using leaf physiognomy

Plotting the ensemble climate data all fossil localities plotted within the temperate forest space; however, the high polar lowland Arctic sites plot along the boundary between temperate forest and temperate rainforest (Fig. 3a). The mid-latitude lowland and upland fossil sites, as well as the low polar lowland site from Alaska, plotted as temperate forests using the physiognomic climate estimates from CLAMP and LAA (Fig. 3b). The high polar lowland fossil localities plot as temperate rainforests when the CLAMP and LAA climate estimates are plotted on biome diagrams (Fig. 3b). However, when the BA climate data are plotted, all fossil localities plot closely within the temperate forest space (Fig. 3c). Results from PCA show that the mid-latitude upland and the Canadian Arctic fossil localities generally plot with modern North American floras (Fig. 4a). The HCA, however, shows the high polar Arctic floras, which group on their own branch, to be dissimilar from modern North American floras (Fig. 4b), whereas the mid-latitude upland floras share some physiognomic characteristics with both the Arctic fossil floras and modern floras from the North American west coast (e.g., Oregon, Washington), and east coast (e.g., Florida, South Carolina). The physiognomic datasets of the Racehorse Creek fossil flora from western Washington and Evan Jones Mine Alaska are not published, and as such were not included in the PCA and HCA analyses of leaf physiognomy.

4. Discussion

4.1 Climate Reconstruction

4.1.1 Mid-Latitude Upland Climate Reconstruction

The ensemble MAT estimates of 7.0–14.9 °C correlates with a cooler to warm temperate climate and agree with previous studies of these upland paleofloras of British Columbia and Washington (Greenwood et al., 2005, Smith et al., 2011; Greenwood et al., 2016; Lowe et al., 2018). However, temperatures below 10 °C imply winters that would have experienced periods of sustained frost, a climate feature that is inconsistent with fossil data (Greenwood et al., 2016). The mean of ensemble MAT estimates, however, suggests an average regional temperature for the

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Okanagan Highlands of ~10 °C, and is more in line with fossil evidence from previous studies (Archibald et al., 2014; Greenwood et al., 2016). The mean ensemble CMMT and WMMT estimates indicate regional temperatures of ~2 °C and ~20 °C, respectively. These estimates suggest that the mid-latitude upland regions in British Columbia and Washington experienced mild winter temperatures (>0 °C) and moderate seasonal changes in temperature. The mean of the ensemble MAP estimates for the Okanagan Highlands suggests an average precipitation of ~110 cm a^{-1}, which indicates mesic conditions (MAP >100 cm a^{-1}), and aligns with fossil evidence that suggest these high-altitude forests were wet-temperate ecosystems (Greenwood et al., 2016). These temperature and precipitation estimates, as well as the compilation of climate data (Table 2 and Tables A1–A3), indicate that the upland regions of British Columbia and Washington experienced a climate during the Eocene similar to the modern day North Pacific coast of North America (e.g., from Vancouver, British Columbia MAT 10.1 °C, CMMT 3.3 °C, WMMT 17.6 °C, MAP 120 cm a^{-1}, 3WET 51 cm, 3DRY 13.2 cm; Environment Canada, 2020; to Portland, Oregon MAT 11.7 °C, CMMT 4.6 °C, WMMT 19 °C, MAP 119 cm a^{-1}, 3WET 47 cm, 3DRY 10.2 cm, NOAA, 2020).

In some cases, site-specific leaf physiognomic-based estimates of MAT were significantly lower than nearby MAT estimates from contemporaneous neighboring fossil localities, and are considered anomalous (e.g., LMA estimates of MAT 2.4 °C from One Mile Creek, B.C. see Table A2). However, as a result of applying our ensemble approach, these anomalous values are muted, as that particular estimate proxy is not weighed as heavily. It is important to note that the early Eocene Okanagan Highland floras of British Columbia and Washington were upland ecosystems; as such, these higher elevation ecosystems would have experienced cooler temperatures than the neighboring lowland fossil localities (e.g., Racehorse Creek) due to temperature lapse with altitude (Wolfe et al., 1998; Greenwood et al., 2016; Lowe et al., 2018).

4.1.2 Mid-latitude Lowland Climate Reconstruction

The ensemble MAT estimates of 17.3–18.9 °C from the lowland Racehorse Creek fossil localities in western Washington indicate a significantly warmer temperature regime compared to the nearby Okanagan Highland upland floras. These MAT estimates, as well as the ensemble CMMT estimates of 7.3–11.4 °C, for Racehorse Creek are in line with thermophilic fossil evidence from the region, including coryphoid palm leaf fossils found in the Chuckanut and Huntingdon formations (Breedlovestrout et al., 2013; Greenwood and Conran, 2019). The palm tribe Coryphoideae, while somewhat cold hardy, is restricted (-2σ) to climates with MAT ≥ 10.3 °C and CMMT ≥ 3.9 °C (Reichgelt et al., 2018). The most recent investigations of the Racehorse Creek fossil flora reported a MAP estimate of 250–360 cm a^{-1} (see Breedlovestrout et al., 2013 and references therein). This is considerably wetter than our ensemble MAP estimate of 135 cm a^{-1} or even the upper 95% confidence interval value of 183 cm a^{-1} (Table 2). These ensemble estimates should potentially be considered as minimum MAP values, as the Racehorse Creek floras were

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lowland coastal environments (Breedlovestrout et al., 2013), and may have experienced more precipitation than estimated here. The compilation of estimated climate data (Table 2 and Tables A1–A3) suggests the lowland regions of western Washington experienced a warm and wet climate during the Eocene similar to regions of the southeast of North America (e.g., Augusta, Georgia, MAT 18.4 °C, CMMT 9.2 °C, WMMT 26.0 °C, MAP ~118 cm a^{-1}, 3WET 36.8 cm, 3DRY 26.5 cm, NOAA, 2020).

4.1.3 High-Latitude Low Polar Climate Reconstruction

The ensemble MAT estimates of 13.3 °C for the Evan Jones Mine flora align with previous studies(e.g., Sunderlin et al., 2011) that indicated these low polar lowland floras were growing under a cooler to warm temperate climate, and similar to a MAT (12.3 °C) estimate by Wolfe (1994). Previously, MAP of the Evan Jones Mine flora had been estimated to be 154.6 cm a^{-1} (Sunderlin et al., 2011). Our ensemble estimate for MAP of 132 cm a^{-1} is a little drier than these prior estimates; however, the upper bound of the 95% confidence interval for the ensemble MAP estimates suggests precipitation could have been considerably wetter (367 cm a^{-1}, Table 2). The ensemble MAT and MAP estimates, coupled with the ensemble CMMT (6.4 °C) and WMMT (21.8 °C) estimates indicate that Alaska experienced some thermal seasonality, mild winter temperatures (>0 °C), and typically wetter conditions than the mid-latitude upland floras of the Okanagan Highlands, but drier than the coastal lowland Racehorse Creek site. The early Eocene climate reconstruction for Alaska is considerably different from the modern-day climate of Alaska, as modern Alaska experiences a cold and dry climate (e.g., Anchorage, AK MAT 2.8 °C, CMMT -8.2 °C, WMMT 14.9 °C, MAP 42.1 cm a^{-1}, 3WET 21 cm, 3DRY 4.5 cm; NOAA, 2020).

4.1.4 High-latitude High Polar Climate Reconstruction

The range of ensemble MAT estimates of 7.6–12.9 °C for the Canadian High Arctic sites agree with previous estimates that indicated these polar lowland floras were growing under a cooler to warm temperate climate. However, similar to the MAT estimates for the upland Okanagan Highland floras, the cooler range of MAT estimates (< 10 °C), would suggest that these high-latitude forests would have experienced periods of sustained frost, an interpretation inconsistent with fossil evidence (see McIver and Basinger, 1999; Eberle and Greenwood et al., 2012; West et al., 2019). The mean of the ensemble MAT estimates of ~10 °C, however, is a more in line with the other proxy evidence for a MAT minimum of the polar regions during the early Eocene, and is a thermal regime supported by fossil evidence mentioned above (McIver and Basinger, 1999; Eberle and Greenwood, 2012; West et al., 2019).

The mean values of the ensemble CMMT and WMMT estimates, ~3 °C and ~18 °C respectively, indicate that the Canadian Arctic experienced moderate thermal seasonality and mild winter temperatures (>0 °C). Previously, MAP for three fossil localities from Ellesmere Island had been estimated to be > 200 cm a^{-1} (e.g., West et al., 2015). New physiognomic estimates of MAP for additional sites from Ellesmere and Axel Heiberg islands produced somewhat drier estimates (~175 cm a^{-1}, Table A2). The ensemble MAP estimates for the Canadian Arctic are also drier than

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the West et al. (2015) physiognomic estimates, ranging from 131–180 cm a^{-1}, with a mean value of ~162 cm a^{-1} (Table 2). These MAP values, though drier than the most recent physiognomic estimates, are still indicative of a wet climate similar to, or wetter than, the Evan Jones Mine flora of Alaska, and wetter still than the mid-latitude lowland and upland floras.

The climate reconstruction for the Canadian Arctic is in stark contrast to the modern-day climate of Ellesmere and Axel Heiberg islands. Ellesmere Island currently experiences a harsh Arctic desert climate (e.g., Eureka, Nunavut MAT -19.7 °C, CMMT -38.4 °C, WMMT 5.7 °C, MAP 7.6 cm a^{-1}, 3WET 3.8 cm, 3DRY 0.82 cm; Environment Canada, 2020). These high-latitude paleoclimate estimates for the Canadian Arctic generally agree with previous high latitude proxy climate data from similarly-aged deposits (Table 3, Fig. 5). However, the physiognomic, BA, and ensemble estimates of this study typically have cooler MAT values, and wetter MAP values than estimates based on stable isotopes or palynofloras (Table 3). Nevertheless, the temperature estimates of this and previous studies indicate that MAT remained relatively homogenous across the high-latitudes throughout the late Paleocene and into the early Eocene (Fig. 5).

4.2 The Latitudinal Temperature Gradient in northern North America

The latitudinal temperature gradient is considered a defining characteristic of the climate system both past and present (Zhang et al., 2019), and is one of the principal factors that control the distribution of vegetation. As such, the persistence of a shallow latitudinal temperature gradient during the early Eocene would have been instrumental in supporting the expansive forest ecosystems that stretched from the mid to high latitudes (Greenwood and Wing, 1995). An understanding of the latitudinal temperature gradient during warm periods in Earth's history remains an integral component of paleoclimate modelling, and relevance of past megathermal intervals as useful analogs for modern global warming (Greenwood and Wing, 1995; Naafs et al., 2018).

However, climate models have had difficulty replicating the shallow latitudinal temperature gradient of the early Eocene (Hollis et al., 2019), with temperatures either unrealistically hot in the tropics, or too cold at the poles and continental interiors. The most successful of these models required pCO_2 of 4480 ppm, which is on the extreme upper end of early Eocene estimates, although CO_2 calibrations tend to lose sensitivity at high values, making quantification difficult (Huber and Caballero, 2011). Paleobotanical proxy methods have been criticized, as differing methods can produce different results (Hollis et al., 2019); however, the ensemble climate estimate method offers considerable improvements for estimating past temperature and precipitation regimes over any single method (e.g., Reichgelt et al., 2018; Lowe et al., 2018; Willard et al., 2019). Therefore, it is important to re-evaluate the latitudinal temperature gradient for northern North America as methodological improvements are made and new data become available.

The modern latitudinal temperature gradient for north-western North America is approximately 1.2 °C/1° latitude (Greenwood and Wing 1995). Previously, paleobotanical data

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from the Western Interior of North America has been used to estimate the latitudinal temperature gradient, which suggested a latitudinal temperature change of 0.30–0.40 °C/1°latitude for the late Paleocene and early Eocene (Greenwood and Wing, 1995; Davies-Vollum, 1997). In addition, prior studies used $\delta^{18}O$ data from coastal marine bivalves to estimate a latitudinal temperature change of 0.28 °C/1° latitude for the late Paleocene and early Eocene in North America (Tripati et al., 2001; Quan et al., 2012, and references therein). Recently, a temperature data compilation of terrestrial climate proxies for the late Paleocene and early Eocene was used to reconstruct a global average latitudinal temperature gradient of 0.16 °C/1° between 30°–60° paleolatitude (Zhang et al., 2019).

As the Okanagan Highlands floras introduce an altitudinal influence, they are not included in an evaluation of the latitudinal temperature gradient. Rather, the temperature estimates from the coastal lowland Racehorse Creek floras are more comparable to the lowland floras of higher latitudes. The ensemble estimates of the lowland Racehorse Creek fossil flora (~48° N) provides a MAT value of ~19 °C. The mean of the ensemble MAT estimates from Ellesmere Island (~80° N), NU, Canada is ~10 °C. The difference in latitude between the two lowland regions is about 31°, which results in a temperature change per degree of latitude of 0.28 °C/1° latitude. The Evan Jones Mine flora (MAT ~13 °C) is located geographically between the lowland fossil localities of Racehorse Creek and Ellesmere Island, and as such appears to indicate that the latitudinal temperature gradient is steeper from the mid-latitudes and shallower in the polar latitudes. The latitudinal temperature gradient estimate of 0.28 °C/1° latitude corroborates estimates previously derived from both paleobotanical and coastal marine sources (Davies-Vollum, 1997; Tripati et al., 2001; Quan et al., 2012). Similar northern hemisphere temperature gradients (0.27 °C/1° latitude) have been estimated from fossil plants for the late Paleocene in China (Quan et al., 2012), which indicate that relatively similar temperature gradients may have been in place globally in the northern hemisphere during the late Paleocene and early Eocene.

4.3 Paleobiomes of northern North America

During the early Eocene, subtropical and temperate forests dominated the mid-latitudes and were comprised of a high diversity of both temperate and thermophilic taxa—with thermophilic floral and faunal elements extending poleward in the Eocene, reaching 70 °N or more (Eberle and Greenwood, 2012). Vegetation models suggest the mid-latitudes were dominated by mixed deciduous and evergreen forests, which is in broad agreement with fossil evidence (Beerling and Woodward, 2001; Shellito and Sloan, 2006). The ability of models calibrated from modern vegetation dynamics to produce results that broadly agree with the fossil record may suggest that ecophysiological controls on plant distributions have not changed markedly during the Cenozoic (Beerling and Woodward, 2001); however, there is still a need to provide a refined and evidence-based interpretation of the forest ecosystems that were in place in northern North America during the early Eocene.

CLAMP climate results for the mid-latitude lowland and upland fossil localities, as well as the high-latitude lowland sites, plot as temperate forest and temperate rainforest biomes (Fig. 3b)

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respectively, but group more tightly within the temperate forest biome when BA climate data are plotted (Fig. 3c). Plotting the ensemble climate estimates from northern North America on biome diagrams (Fig. 3b), however, further demonstrates the similarity in both vegetation and climate throughout these regions. The majority of the fossil localities plot within the climate space to be classified as temperate forest ecosystems (Fig. 3), with two high-latitude localities plotting on the boundary between temperate forest and temperate rainforest ecosystems. Whipsaw Creek, a fossil locality of the Okanagan Highlands (Table 1), plots as a grassland biome; however, when the upper end of the errors are considered, this fossil locality overlaps with the fossil localities plotted as temperate forests.

Temperature and precipitation correlate positively with the rate of productivity in a forest (Whittaker, 1975). Therefore, the standing biomass and annual net primary productivity of a forest will differ depending on the climatic zone. Typically, temperate forests have an average above-ground net primary productivity (ANPP) of about 9.5 Mg ha^{-1} yr^{-1} (Saugier et al., 2001), but this value can differ based on the regional climate. For example, temperate rainforests from the Pacific Northwest with MAP values of > 150 cm a^{-1} have been shown to have an above-ground biomass of 467–1316 Mg ha^{-1} and an annual net primary productivity of 4.2-15 Mg ha^{-1} yr^{-1} (Gholz, 1982), whereas wetland forests such as the *Taxodium* (swamp cypress) dominated forests of Florida, have been shown to have an above-ground biomass of 284 Mg ha^{-1} and an ANPP of 16.1 Mg ha^{-1} yr^{-1} (Brown, 1981). Temperate broad-leaved forests from Tennessee typically have an above-ground biomass of 326–471 Mg ha^{-1} and an ANPP of 6.3–13.1 Mg ha^{-1} y^{-1} depending on the age of the forest stand (Busing, 2013). Biomass and ANPP has been previously reconstructed as 501-587 Mg ha^{-1} and 5.8-7.8 Mg ha^{-1} yr^{-1}, respectively, for the late Paleocene to early Eocene *Metasequoia* (dawn redwood) dominated swamp forests of Stenkul Fiord (Williams et al., 2009). Above-ground biomass has also been reconstructed as 946 Mg ha^{-1} for the middle Eocene forests on Axel Heiberg Island (Basinger et al., 1994). These values fall within the range of values appropriate for modern temperate forests, and the lower to middle range for the temperate rainforests of the Pacific Northwest, which suggests that modern values of biomass and ANNP may be useful approximations for model simulations if the forest biome is known.

Our data support previous studies that have described the upland fossil megaflora of British Columbia and Washington state as having a dominant temperate component, or belonging to a temperate forest ecosystem with analogues from modern west coast temperate forest ecosystems (Greenwood et al., 2016; Lowe et al., 2018). These upland paleofloras reflect forests consisting of mixed temperate and tropical plants, with insects (e.g. lacewings and palm beetles), birds and mammals (e.g. hedgehogs and tapirs) (Archibald et al., 2011; Greenwood et al., 2005, 2016; Eberle et al., 2014; Eberle and Greenwood, 2017). The ancient plant communities were diverse and are typically dominated by taxa such as *Ginkgo*, Pinaceae such as *Picea* (spruce), Cupressaceae such as *Metasequoia* (dawn redwood), *Sassafras*, *Betula* (birch), *Alnus* (alder), *Ulmus* (elm), *Cercidiphyllum*/*Trochodendroides* (katsura), and rare palms (Smith et al., 2009; DeVore and Pigg 2007, 2010; Greenwood et al., 2005, 2016; Mathewes et al., 2016; Lowe et al., 2018). During the

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early Eocene, more southerly regions of North America hosted mainly tropical flora and fauna, supported by warmer climate conditions than those of the Okanagan Highlands (Archibald et al., 2010; Morley, 2011; Eberle and Greenwood, 2012), more similar in climate to the lowland Racehorse Creek flora from western Washington (DeVore and Pigg 2010; Beedlovestrout et al., 2013), fossil floras of the Green River Basin (Wolfe, 1994; Wilf, 2000), and to the southeast (Currano et al., 2010) in the U.S.A.

The lowland Canadian Arctic megafloras have previously been described as representing a temperate rainforest based on leaf physiognomic climate estimates (e.g., Greenwood et al., 2010; West et al., 2015), an interpretation supported by the leaf physiognomic climate estimate biome plots (Fig. 3), and the fossil taxa present (McIver and Basinger, 1999; Eberle and Greenwood, 2012; West et al., 2019). The early Eocene polar broadleaf deciduous fossil forests of Alaska and those of Ellesmere and Axel Heiberg islands in Arctic Canada reflect a mixed temperate flora (*Ulmus*, *Alnus*, *Tetracentron*, *Magnolia*), with some rare tropical elements (palynological evidence for palms found in the ACEX cores; McIver and Basinger, 1999; Sluijs et al., 2009; Sunderlin et al., 2011; Salpin et al., 2018; West et al., 2015, 2019; Willard et al., 2019). Prior vertebrate paleontological studies from the region have shown that these polar environments were also host to a mix of fauna that included alligators and thermophilic forms of, snakes, turtles, large mammals, terror birds, and early primates (Estes and Hutchinson, 1980; McKenna, 1980; Dawson et al., 1993; Eberle, 2005; Eberle et al., 2014).

Results from PCA show that the mid- and high-latitude lowland fossil localities generally plot with the North American and Eurasian floras (Fig. 4a). Despite this, the leaf physiognomy-based HCA indicates that the Arctic fossil floras are physiognomically distinct from modern floras (Fig. 4b). The mid-latitude floras appear to share some leaf physiognomic characteristics with both the Arctic fossil floras and modern floras from the North American west coast (e.g., Oregon, Washington), and east coast (e.g., Florida, South Carolina). The physiognomic distinctiveness of the Eocene Arctic floras from both modern floras and mid-latitude Eocene floras may be due to an ancient environment with no modern analog, due to the extreme abiotic stress from photic seasonality combined with high precipitation and relatively mild temperatures (e.g., West et al. 2015, and references therein). Forests cannot currently occur at such high latitudes, and therefore these physiognomic responses and adaptations have no modern analogue; thus, these polar ecosystems can be referred to as fossil, or extinct ecosystems (West et al. 2015, and references therein). These results, coupled with the ensemble climate estimates, suggest considerable climatic overlap existed between the mid- and high-latitudes during the early Eocene. This suggests that the similar climatic regimes, facilitated by a shallow latitudinal temperature gradient, allowed for similar forest ecosystems—both floristically and vegetatively—to exist at both mid- and high-latitudes during the early Eocene, despite substantial differences in latitude and photic seasonality.

5 Conclusions

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The results of our ensemble approach to climate reconstruction for the mid- and high latitudes of northern North America describe a low latitudinal temperature gradient (0.28 °C/1° latitude) and broad climatic similarity across a large latitudinal range (~30°) during the early Eocene, although variation in precipitation between the mid- and high latitudes is evident (Fig. 5). This shallow latitudinal temperature gradient supported an extensive forest ecosystem that spanned most of northern North America from Washington USA to Ellesmere Island, NU, with several genera occurring throughout its entire extent (e.g., *Metasequoia*, *Alnus*, *Ulmus*; see West et al., 2019). The climate estimates derived from the upland fossil floras of the mid-latitude sites in Washington and British Columbia, coupled with biome charts and physiognomic analysis, indicate that these ancient forests ecosystems share physiognomic features with modern temperate forests from the Pacific Northwest. The high-latitude lowland fossil localities from Arctic Canada plot with as temperate forests, alongside fossil floras from the mid-latitudes, but exist at the boundary between the climatic range for a temperate forest and temperate rainforest. Although, in the HCA analysis, the physiognomic character of the Arctic forests was dissimilar from modern forest ecosystems, whereas the mid-latitude fossil sites share more physiognomic qualities with modern forests and the early Eocene polar forests—potentially resulting from similar climatic conditions. Despite the antiquity of these forest ecosystems, the PCA analysis of fossil site physiognomy of both the mid- and high-latitude sites demonstrates that these forests broadly group with modern floras from North America and Eurasia.

These results indicate that the climate of northern North America during the early Eocene was potentially more homogenous than previously appreciated, and capable of supporting climatically, and taxonomically, similar forests at mid- and high latitudes, supported by a shallow latitudinal temperature gradient. Although PCA of the physiognomic character of the Arctic forests broadly groups with modern forest ecosystems, the results of the HCA analysis indicate that these ancient forests do not align physiognomically with any modern forest ecosystem, this is not unexpected as these high-latitude ecosystems would have experienced pronounced photic seasonality and an enhanced hydrological cycle during Eocene warmth (see West et al., 2015 and references therein)—which resulted in an ecosystem that has since become extinct.

Improved terrestrial climate estimates and vegetation resulting from an ensemble approach offer opportunities to better classify these ancient forest ecosystems, enhancing utility of the paleobotanical record for paleoclimate modeling. This is a step towards meeting the goals recommended by Hollis et al. (2019) and the modelling community (e.g., DeepMIP; Hollis et al. 2019; Lunt et al., 2020) in striving to improve the quality and clarity of proxy data and derived climatic parameters.

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Figure 1: Location map showing the location of the fossil localities used in this study. **(**1) Lake Hazen, (2) Mosquito Creek, (3) Ox-Head Creek, (4) Hot Weather Creek, (5) Fosheim Anticline, (6) Strand Fiord), (7) Strathcona Fiord, (8) Split Lake, (9) Stenkul Fiord, (10) Evan Jones Mine, (11) Chu Chua, (12) McAbee, (13) Quilchena, (14) Falkland, (15) Thomas Ranch, (16) One Mile Creek, (17) Whipsaw Creek, (18) Republic, (19) Racehorse Creek.

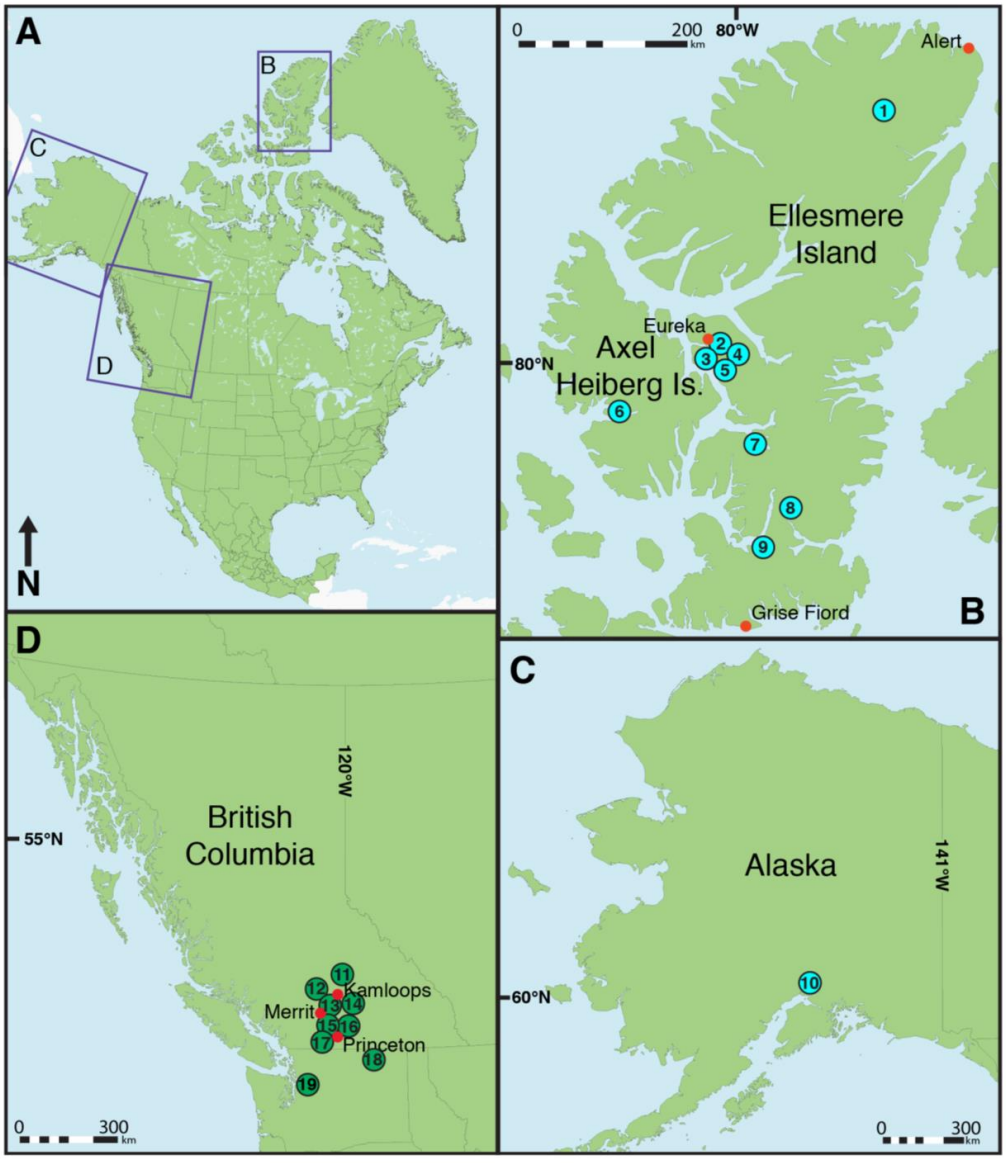

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Figure 2: Stratigraphic compilation of corresponding formations for the fossil localities used in this study. A-F represent the corresponding radiometric data for those formations, and leaf images numbered 1-6 represent approximate stratigraphic positions of the floras used for this study. Data compiled from Sunderlin et al., 2011, Breedlovestrout et al., 2013, Greenwood et al., 2016, and West et al., 2015. Modified from West et al., 2019 and Greenwood et al., 2016.

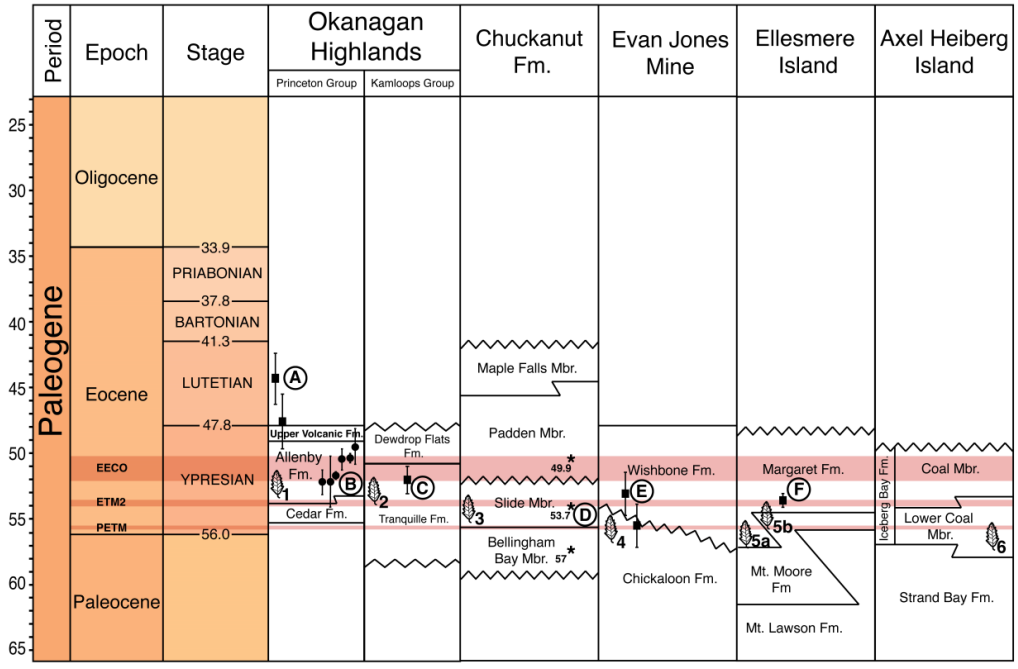

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Figure 3: Biome charts showing the paleoclimate data plotted against modern climate parameters defining modern biomes. (A) Ensemble climate estimates, (B)Leaf physiognomy estimates, (C) BA estimates.

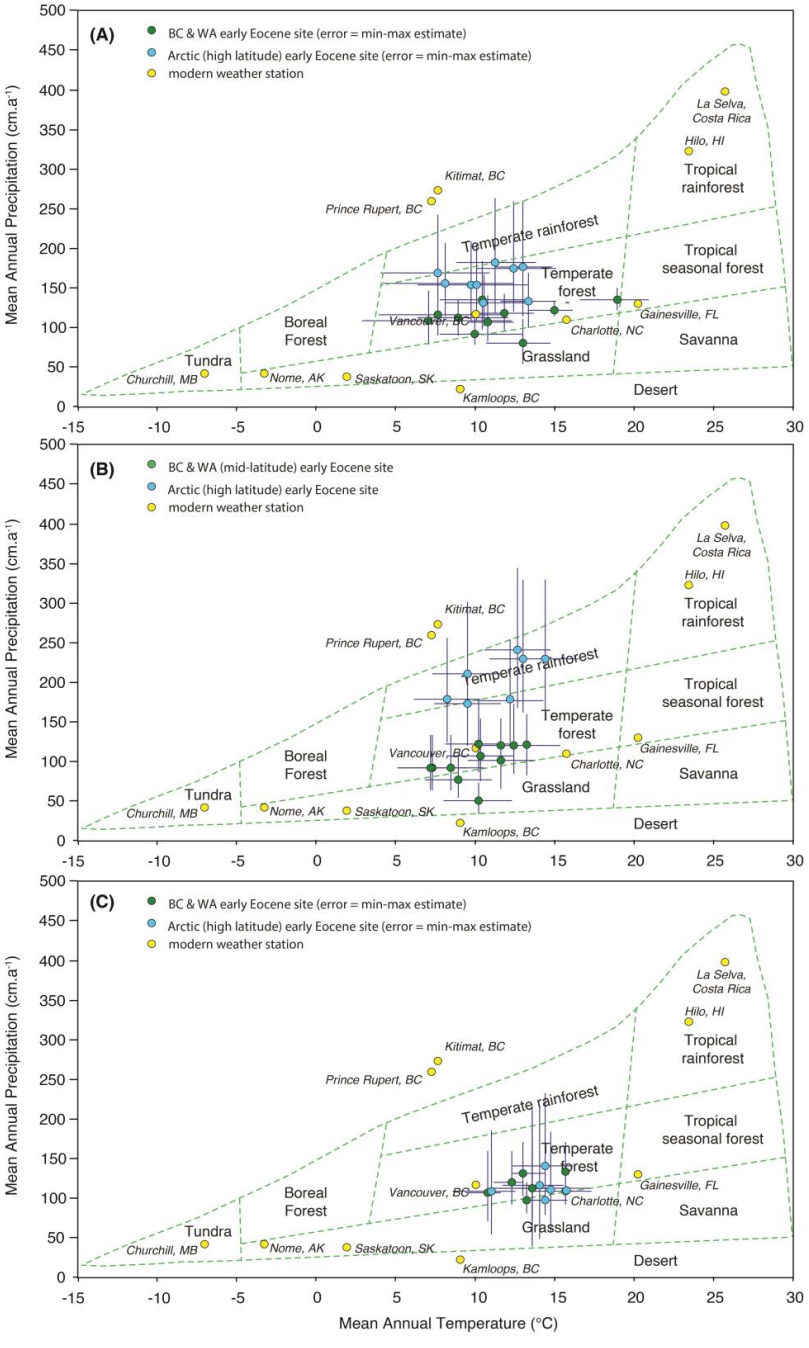

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Figure 4: PCA and HCA analysis using CLAMP derived physiognomic data from the fossil floras used for this study. (A) PCA showing how the fossil floras group with modern floras based on leaf physiognomy. PCA axis 1 explains 41.3% of the variance, and PCA axis 2 explains 26.3% of the variances. Blue triangles represent the Canadian Arctic localities. Green circle represent the Okanagan Highlands upland localities. (B) HCA graph showing how the fossil floras group compared against modern floras. Blue text refers to the Canadian Arctic fossil localities. Green text refers to the Okanagan Highland upland fossil localities. Purple text refers to modern sites from North America. Orange text refers to modern sites from Eurasia.

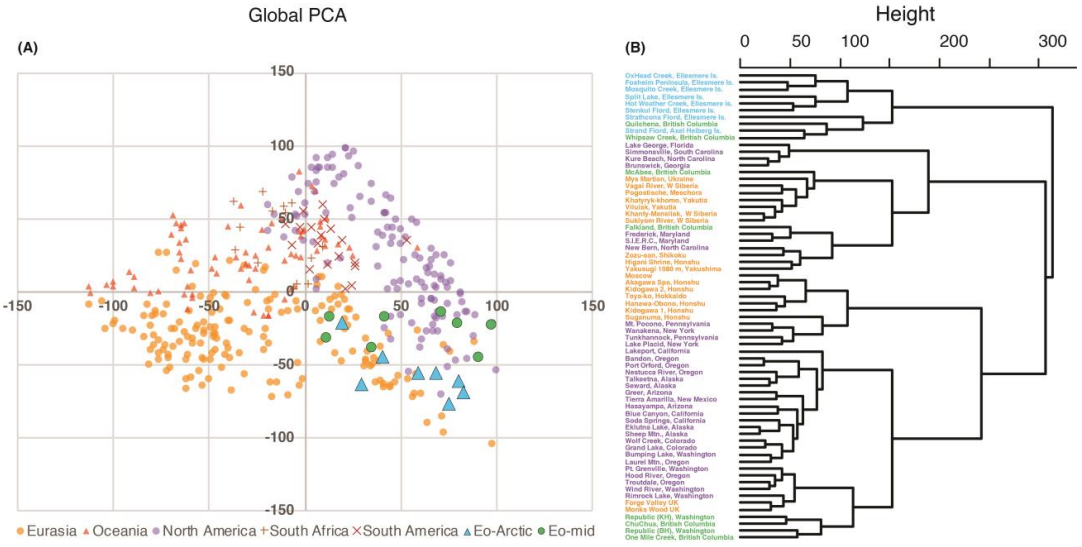

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Figure 5: Proxy ensemble data from fossil localities showing (**A**) MAT and (**B**) MAP estimates from this study, and prior studies compiled in Table 3.

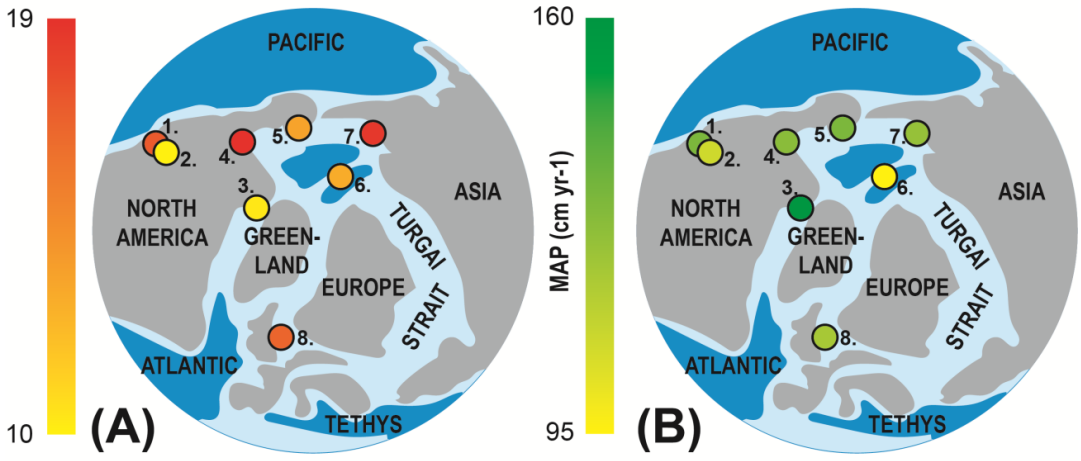

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Table 1: Locality information of fossil sites discussed in this study. BC – British Columbia, Canada; NU – Nunavut, Canada; WA – Washington, USA; AK – Alaska, USA.

Area	*Fossil site*	*Rock unit*	*Age*	*Modern Latitude*	*Information sources*
WA	Republic	Klondike Fm.	early Eocene	48.3	Wolfe et al., 1998; This study;
WA	Racehorse Creek	Slide Mbr, Chuckanut Fm.	early Eocene	48.4	Breedlovestrout 2011; Breedlovestrout et al., 2013
BC	One Mile Creek	Allenby Fm.	early Eocene	49.2	Wolfe et al., 1998; Greenwood et al., 2016; This study
BC	Thomas Ranch	Vermillion Bluffs Shale, Allenby Fm.	early Eocene	49.2	Dillhoff et al., 2013
BC	Whipsaw Creek	Vermillion Bluffs Shale, Allenby Fm.	early Eocene	49.2	Greenwood et al., 2016; This study
BC	Quilchena	Coldwater Beds	early Eocene	50.1	Mathews et al., 2016; This study
BC	Falkland	Tranquille Fm.	early Eocene	50.3	Smith 2011; Smith et al., 2009, 2012
BC	McAbee	Tranquille Fm.	early Eocene	50.4	Gushulak et al., 2016; Lowe et al., 2018
BC	Chu Chua	Chu Chua Fm.	early Eocene	51.2	Wolfe et al., 1998; Greenwood et al., 2016; This study
AK	Evan Jones Mine	Chickaloon Fm.	late Paleocene to early Eocene	61.4	Sunderlin et al., 2011
NU	Stenkul Fiord	Margaret Fm.	late Paleocene to early Eocene	77.2	West et al., 2015
NU	Split Lake	Mt Moore Fm.	late Paleocene to early Eocene	77.5	West et al., 2015
NU	Strathcona Fiord	Mt Moore Fm.	late Paleocene to early Eocene	78.3	West et al., 2015
NU	Strand Fiord	Iceberg Bay Fm.	late Paleocene to early Eocene	79.1	West et al., 2019; This study

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NU	Fosheim Anticline	?Mt.Moore/?Margaret Fm.	late Paleocene to early Eocene	79.4	West et al., 2019; This study
NU	Hot Weather Creek	?Mt.Moore/?Margaret Fm.	late Paleocene to early Eocene	79.4	West et al., 2019; This study
NU	Mosquito Creek	?Mt.Moore/?Margaret Fm.	late Paleocene to early Eocene	79.5	West et al., 2019; This study
NU	Ox-Head Creek	?Mt.Moore/?Margaret Fm.	late Paleocene to early Eocene	79.5	West et al.; This study
NU	Lake Hazen		late Paleocene to early Eocene	81.4	West et al., 2019; This study

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Table 2: Proxy ensemble climate estimates for fossil plant localities. Bracketed range indicates the 95% confidence interval of the bootstrapped paleobotanical proxy estimates.

Localities	*MAT* (°C)	*WMMT* (°C)	*CMMT* (°C)	*MAP* (cm a^{-1})
WA Republic (BH)	7.6 (-0.5-14.3)	18.9 (13.6-24.0)	1.6 (-6.3-7.2)	116 (48-293)
WA Republic (KH)	11.8 (5.0-18.1)	20.6 (17.0-25.2)	2.3 (-5.0-8.7)	118 (51-332)
WA Racehorse Creek	17.3 (10.4-25.4)	23.6 (18.6-28.5)	7.3 (0.3-13.9)	---
WA Racehorse Creek (Landslide)	18.9 (11.6-26.1)	23.1 (19.6-27.8)	11.4 (3.5-17.0)	135 (100-183)
BC One Mile Creek	7.0 (-0.9-13.6)	19.2 (14.6-22.7)	-0.3 (-9.4-5.8)	109 (43-362)
BC Thomas Ranch	9.9 (4.5-13.6)	20.0 (15.9-24.0)	1.1 (-6.8-5.6)	92 (42-140)
BC Whipsaw Creek	13.0 (6.5-21.2)	20.4 (15.8-25.2)	1.2 (-2.8-6.7)	80 (29-244)
BC Quilchena	14.9 (8.10-21.2)	22.7 (18.9-27.1)	5.3 (-1.6-9.8)	121 (62-186)
BC Falkland	10.4 (2.3-15.9)	20.8 (17.4-21.7)	4.3 (-1.5-9.9)	135 (52-416)
BC McAbee	10.8 (4.0-16.7)	20.7 (16.2-27.2)	1.8 (-4.5-8.5)	106 (33-315)
BC Chua Chua	8.9 (1.9-15.0)	18.6 (13.0-21.7)	0.0 (-8.3-5.6)	113 (49-292)
AK Evan Jones Mine	13.3 (7.7-17.6)	21.8 (17.2-26.2)	6.4 (0.8-12.2)	132 (63-367)
NU Stenkul Fiord	11.2 (3.1-17.4)	21.4 (17.6-26.5)	4.0 (-1.8-9.8)	180 (81-549)
NU Split Lake	12.4 (3.4-19.1)	22.2 (13.4-28.8)	3.8 (-5.5-11.2)	174 (63-501)
NU Strathcona Fiord	12.9 (5.2-19.6)	21.8 (18.0-27.1)	4.2 (-1.8-10.5)	175 (78-539)
NU Strand Fiord	10.5 (1.8-17.5)	20.3 (15.7-25.4)	2.7 (-4.4-9.7)	131 (61-374)
NU Fosheim Anticline	10.0 (1.2-16.8)	19.8 (14.0-24.8)	3.1 (-4.7-9.7)	152 (73-442)
NU Hot Weather Creek	9.7 (-0.2-17.0)	20.2 (14.7-25.0)	3.9 (-2.4-11.3)	153 (66-444)
NU Mosquito Creek	7.6 (-0.8-15.0)	18.2 (13.5-23.9)	1.3 (-6.0-7.8)	168 (64-488)
NU Ox Head Creek	8.0 (-1.0-17.0)	19.1 (14.1-24.9)	2.3 (-7.9-11.2)	155 (69-432)

https://doi.org/10.5194/cp-2020-32
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Table 3: Compiled Arctic temperature proxy data from additional sources.

Fossil locality	MAT °C	WMMT °C	CMMT °C	MAP cm a^{-1}
North Sea[1]	16.0-17.0	~25.0	10.2	>120
Mackenzie Delta[2]	16.0-25.0	25.0-28.0	5.0*15.5	110-160
New Siberian Islands[3]	16.0-21.0	25.0-28.0	5.5-14.0	110-140
Lomonosov Ridge[4]	10.8-14.7	17.9-20.2	3.5-8.9	89.8-97.5

1. Eldrett et al., 2014
2. Salpin et al., 2018
3. Suan et al., 2017
4. Willard et al., 2019

https://doi.org/10.5194/cp-2020-32
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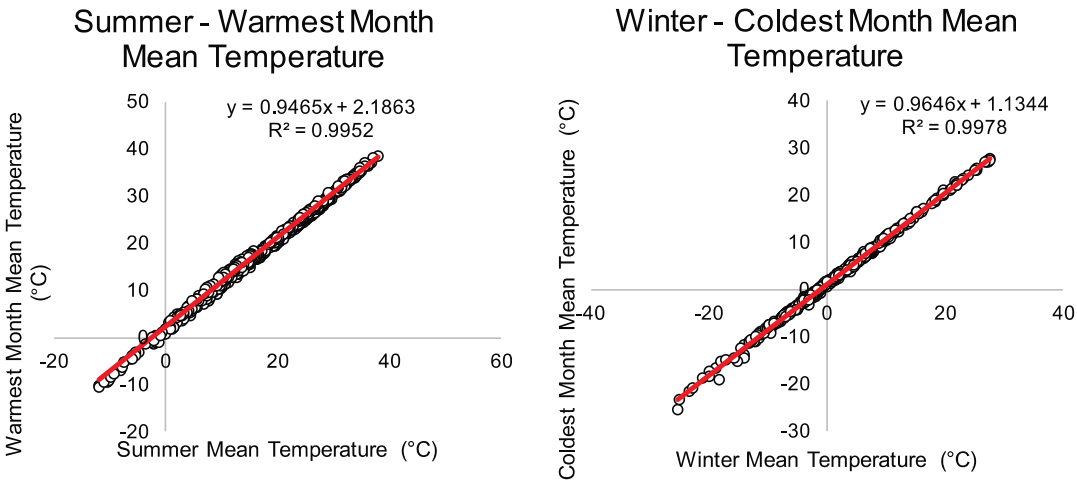
6. Appendix A

Figure A1: Correlation between Summer and Warmest Month Mean Temperature, and Winter and Coldest Month Mean Temperature (Reichgelt et al., 2018). This correlation was used to compare Bioclimatic Analysis results to CLAMP results, as the former uses Summer/Winter Mean, and the latter uses Warmest and Coldest Month Means.



https://doi.org/10.5194/cp-2020-32
Preprint. Discussion started: 24 March 2020

Table A1: CLAMP derived paleoclimate estimates. Unless otherwise specified, data are original to this study. See Table 1 for locality data. Standard errors and units for climate parameters: MAT ± 2.1°C; CMMT ± 3.4 °C; WMMT ± 2.5 °C; LGS ± 1.1 months; GSP ± 32 cm; 3-WET ± 23 cm; 3-DRY ± 6 cm; RH ± 8.6%; SH ± 1.7 g/kg.

Localities	*n*	*MAT*	*CMMT*	*WMMT*	*LGS*	*GSP*	*3-WET*	*3-DRY*	*RH*
Republic (Boot Hill)	27	8.5	-0.8	17.9	5.4	74.6	66.1	11.5	66.4
Republic (Knob Hill)	43	10.4	0.6	21	6.4	79.9	57.2	15.9	73.2
Racehorse Creek (LS)	--	16	8.7	23.6	8.9	123	58.7	23.4	81
Racehorse Creek	??	15.3	7.3	23.6	8.6	127	58.7	25.9	82.7
One Mile Creek	25	7.2	-3.8	18.5	4.8	48.7	51.5	11.8	69.3
Thomas Ranch	31	9	-1.2	20	5.8	68	40	23.3	67.2
Whipsaw Creek	36	10.2	-0.3	21.1	6.3	100	65.6	20.5	76.9
Quilchena	55	13.3	4.1	23.1	7.7	117	64.7	20.2	76.5
Falkland (combined)	70	12.5	4.3	21.7	7.2	85	49.3	28.9	77
McAbee	43	11.7	1.3	22.9	6.9	113	65.4	19.9	75.5
Chu Chua	27	7.3	-2.5	17.4	4.6	67	62.6	21.2	65.5
Evan Jones Mine	??	13.7	6.1	22.2	7.7	118	63.5	36.6	--
Stenkul Fiord	25	12.7	3.6	22	7.5	90	46.2	26.5	84
Split Lake	11	14.4	4.6	24.4	8.4	96	39.1	31.3	84.2
Strathcona Fiord	15	13	4.0	22.3	7.7	111	54.4	27	83.6
Strand Fiord	15	10.3	1.0	19.8	6.3	76	52	19.7	79.7
Fosheim Anticline	15	9.6	0.8	18.1	6.1	61	44.5	21.8	82.9
Hot Weather Creek	10	12.2	3.6	20.8	7.3	80	44.1	25.7	84
Mosquito Creek	13	9.5	0.5	18.1	6.1	45	36.9	21.5	83.4
Ox Head Creek	13	8.3	-2.1	18.6	5.5	44	37.6	21.2	82.8

n = number of leaf morphotypes scored; MAT = Mean annual temperature; CMMT = Cold month mean temperature; WMMT = Warm month mean temperature; LGS = Length of growing season; GSP = Growing season precipitation; 3-WET = Precipitation during the three consecutive wettest months; 3-DRY = Precipitation during the three consecutive driest months; RH = Relative humidity.

https://doi.org/10.5194/cp-2020-32
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Table A2: Paleoclimate estimates from leaf margin analysis (LMA: Wing & Greenwood 1993; Wilf 1997; Peppe et al., 2011) and leaf area analysis (LAA: Wilf et al., 1998; Peppe et al., 2011). Unless otherwise specified, data and estimates original to this study. See Table 1 for locality data. Errors stated within the table; errors for MAP are asymmetric as they are converted from $\log_e$. Where *n* has two values, different *n* applies to LMA/LAA due to overly incomplete leaves being excluded from LAA.

Localities	*n*	*LMP*	*MAT-1*	*MAT-2*	*MLnA*	*MAP-3*	*MAP-4*
Republic (BH)	27	0.07	3.4 ± 1.5	6.1 ± 4.8	6.9	93 +40, -28	130 +109, -59
Republic (KH)	43	0.35	11.8 ± 2.2	11.7 ± 4.8	7.1	108 +47, -33	140 +118, -64
Racehorse Ck (LS) ††	32	0.67	21.9 ± 2.6	18.4 ± 4.8	--	--	--
Racehorse Creek††	23	0.61	19.8 ± 3.1	17.0 ± 4.8	--	--	--
One Mile Creek	24/25	0.04	2.4 ± 1.2	5.4 ± 4.8	6.9	93 +40, -28	130 +109, -59
Thomas Ranch‡‡	31	0.21	7.8 ± 2.1	--	--	77 +33, −23	--
Whipsaw Creek	24	0.46	15.2 ± 3.1	14 ± 4.8	6.1	51 +22, -16	95 +80, -43
Quilchena++	55	0.49	16.2 ± 2.0	14.6 ± 4.8	--	121 ± 39	--
Falkland*	59	0.2	7.3 ± 2.0	8.7 ± 4.8	7.4	121 +52, -37	149 +125, -68
McAbee+	43	0.3	10.2 ± 2.5	10.6 ± 4.8	6.7	87 +76, -8	125 +105, -57
Chu Chua	24	0.19	6.9 ± 2.4	8.4 ± 4.8	6.9	93 +40, -28	130 +109, -59
Evan Jones Mine‡	39	0.321	11.0 ± 2.3	--	7.6	155 +108,-221	--
Stenkul Fiord†	25	--	8.5 ± 2.6	9.5 ± 4.8	8.6	240 + 104, -72	211 +178, -96
Split Lake†	11	--	10.9 ± 4.3	11.1 ± 4.8	8.5	230 +99, -69	207 +174, -94
Strathcona Fiord†	15	--	12.4 ± 3.8	12.1 ± 4.8	8.5	230 +99, -69	207+174, -94
Strand Fiord	15/13	0.23	8.2 ± 3.6	9.3 ± 4.8	7.4	123 +53, -37	150 +126, -68,
Fosheim Anticline	15	0.2	7.3 ± 3.2	8.7 ± 4.8	8	173 +75, -52	178 +149, -81
Hot Weather Creek	10/9	0.15	5.7 ± 3.5	7.7 ± 4.8	8	177 +77, -53	181 +151, -82
Mosquito Creek	13/10	0.7	3.3 ± 2.1	6.1 ± 4.8	8.4	210 +91, -63	197 +165, -90
Ox-Head Creek	13/11	0.8	3.5 ± 2.3	6.2 ± 4.8	8.1	178 +77, -54	181 +152, -82

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n = number of dicot leaf morphotypes scored; LMP = leaf margin proportion (number of non-toothed leaf morphotypes as proportion of *n*: $0 > X \leq 1.0$; Wilf, 1997); MAT = Mean annual temperature; MAT-1 = LMA equation of Wing and Greenwood, 1993; MAT-2 = LMA global equation of Peppe et al., 2011; MLnA = mean leaf size expressed as $\log_e$; MAP = mean annual precipitation, where MAP-3 = LAA equation of Wilf et al., 1998; MAP-4 = LAA global equation of Peppe et al., 2011.

†† Breedlovestrout et al., 2013.
‡‡ Dillhoff et al., 2013
++ Mathewes et al., 2016
* Smith et al., 2011.
+ Lowe et al., 2018.
‡ Sunderlin et al., 2011.
† West et al., 2015.

https://doi.org/10.5194/cp-2020-32
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Table A3: Paleoclimate estimates using NLR-based BA method.

Localities	*min MAT*	*mean MAT*	*max MAT*	*minSumT*	*mean SumT*	*maxSumT*	*minWinT*	*mean WinT*	*max WinT*	*minMAP*	*mean MAP*	*max MAP*
Republic Boot Hill	11.8	13.1	13.9	19.5	21	23.2	2.3	6.0	7.1	112.2	131.8	151.4
Republic - Knob Hill	12.7	13.6	14.2	20.2	21.3	22.4	3.2	4.8	7.6	100.0	112.2	131.8
Racehorse Ck (Slide Mbr)	18.4	19.4	20.4	22.3	23.6	24.8	13.2	14.3	16.3	114.8	134.9	158.5
One Mile Creek	12.0	13.6	13.6	19.8	21.3	22	2.3	4.8	6	97.7	112.2	120.2
Thomas Ranch	12.4	13.6	13.6	20.2	21.3	22	2.9	4.8	5.8	97.7	112.2	120.2
Whipsaw Creek	10.8	13.3	13.6	18.7	21	22.6	1.0	4.4	6.4	85.1	97.7	128.8
Quilchena	15.4	15.7	15.7	23	23	23.7	7.0	7.0	7.7	117.5	131.8	131.8
Falkland	12.6	13.6	13.6	20.2	21.3	21.3	4.8	4.8	6.2	102.3	112.2	117.5
McAbee	10.0	10.8	12.2	18.2	19.2	21.3	0.8	2.8	5.4	89.1	107.2	128.8
Chua Chua BC	11.8	12.4	13.6	19.8	21.5	22.0	2.2	2.9	5.0	104.7	120.2	131.8
Evan Jones Mine	13.9	14.8	16.4	20.7	23.1	24.0	5.5	7.1	9.6	91.2	109.6	144.5
Stenkul Fiord	12.7	13.6	15.6	20.3	21.3	24.2	3.1	4.8	7.7	95.5	112.2	131.8
Split Lake	10.0	13.6	15.6	17.3	21.3	24.7	-0.1	4.8	9.0	77.6	112.2	154.9
Strathcona	11.1	13.6	15.7	18.4	21.3	24.4	2.0	4.8	8.7	89.1	112.2	151.4
Strand Fiord	12.3	13.6	16.0	20.1	21.3	24.1	3.2	4.8	9.0	95.5	112.2	147.9
Fosheim Anticline	12.3	14.8	16.0	20.1	23.1	24.7	3.2	7.1	9.1	95.5	109.6	144.5
Hot Weather Creek	11.1	13.6	15.7	18.4	21.3	24.3	1.8	4.8	8.9	89.1	112.2	154.9
Mosquito Creek	9.6	11.1	13.6	17.3	19.1	22.6	-0.5	3.9	6.7	81.3	109.6	147.9
Oxhead Creek	12.6	14.1	16.4	18.8	20.3	23.7	4.8	8.1	10.4	95.5	117.5	144.5
Lake Hazen	12.6	14.4	16.4	19.5	22.2	24.0	3.9	6.9	9.8	95.5	141.3	144.5

minMAT = minimum mean annual temperature; *meanMAT* = average mean annual temperature; *maxMAT* = maximum mean annual temperature; *minSumT* = minimum summer temperature; *meanSumT* = average summer temperature; *maxSumT* = maximum summer temperature; *minWinT* = minimum winter temperature; *meanWinT* = average winter temperature; *maxWinT* = maximum winter temperature; *minMAP* = minimum mean annual precipitation; *meanMAP* = average mean annual precipitation; *maxMAP* = maximum mean annual precipitation.

7. Author contributions

CKW and DRG conceived the study. CKW led the writing and co-ordinated the analyses. CKW, JMV, AJL, and JFB collected the samples, and CKW, TR, AJL and JMV collected and analysed the data. CKW, DRG, and JFB wrote the paper with inputs from all of the authors.

8. Competing interests

The authors declare that they have no conflicts of interest.

10. Acknowledgements

Field work in B.C. and Arctic Canada was under scientific and paleontological collection permits issued by the B.C. and Nunavut governments where required. DRG and JMV thank K. Pugh for the loan of his Whipsaw Creek fossil collection and for site information. We thank R.Y. Smith and R.L. Love (formerly Breedlovestrout) for the provision of CLAMP analyses from their PhD work. This work includes research from the Doctoral dissertation of CKW at the University of Saskatchewan, and the Master of Science theses of JMV and AJL at Brandon University. DRG, CKW and TR thank D. Lunt, C. Hollis and M. Huber for suggestions on the scope of the paper.

Financial support. This work was substantially supported by: the Natural Sciences and Engineering Research Council of Canada (NSERC) through Discovery Grants (DG 311934 and 2016-04337) to DRG, a Doctoral Scholarship (Alexander Graham Bell Doctoral Scholarship) to CKW; a grant from the Brandon University Research Committee to DRG for Arctic field work; Geological Society of America student research grants to CKW (11816-17) and to JMV (12565-19), and Paleontological Society and SEPM graduate awards to AJL, and a National Geographic Society Exploration Grant (9652-15) to DRG (S.B. Archibald and J. Eberle co-PIs), and a Vetlesen Foundation Climate Center grant to TR, all for field work support in British Columbia. DRG acknowledges support from the Canada Foundation for Innovation (project 31801) and Research Manitoba for laboratory facilities at Brandon University used in this study, and Brandon University Student Union for student employment grants for two B.C. field seasons. Arctic fieldwork by JFB was supported by NSERC (DG 1334) and the Polar Continental Shelf Program.

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