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Research Article

Reconstruction of climate and ecology of Skagit Valley, Washington, from 27.7 to 19.8 ka based on plant and beetle macrofossils

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Abstract

Glacial lake sediments exposed at two sites in Skagit Valley, Washington, encase abundant macrofossils dating from 27.7 to 19.8 cal ka BP. At the last glacial maximum (LGM) most of the valley floor was part of a regionally extensive arid boreal (subalpine) forest that periodically included montane and temperate trees and open boreal species such as dwarf birch, northern spikemoss, and heath. We used the modern distribution and climate of 14 species in 12 macrofossil assemblages and a probability density function approach to reconstruct the LGM climate. Median annual precipitation (MAP) at glacial Lake Concrete (GLC) was ~50% lower than today. In comparison, MAP at glacial Lake Skymo (GLS) was only ~10% lower, which eliminated the steep climate gradient observed today. Median January air temperature at GLC was up to 10.8°C lower than today at 23.5 cal ka BP and 8.7°C lower at GLS at 25.1 cal ka BP. Median July air temperature declines were smaller at GLC (3.4°C–5.0°C) and GLS (4.2°C–6.3°C). Warmer winters (+2°C to +4°C) and increases in MAP (+200 mm) occurred at 27.7, 25.9, 24.4, and 21.2–20.7 cal ka BP. These changes accord with other regional proxies and Dansgaard–Oeschger interstades in the North Atlantic.

Keywords: Last glaciation, Macrofossils, Paleoecology, Paleoclimate, Skagit Valley, Washington, North Cascades

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INTRODUCTION

Climate change has reorganized ecosystems throughout our planet's history (Gavin et al., 2014). Recognizing how ecosystems have responded to past changes in climate helps us understand the impact of future climate change (Harrison and Sanchez Goni, 2010). The last glacial maximum (LGM) represents an extreme state of climate from 26.5 to 19 cal ka BP, when Northern Hemisphere solar insolation and CO_2 levels in the atmosphere were low, global mean temperature was 4 ± 0.8°C cooler than today, and continental glaciers were near their maximum extents (Berger, 1978; Clark et al., 2009; Annan and Hargreaves, 2013). On millennial or shorter time scales, this period was marked by changes in temperature and precipitation that punctuated the overall dry, cold LGM climate of the Pacific Northwest (Grigg and Whitlock, 2002; Jiménez-Moreno et al., 2010; Oster et al., 2015). The millennial-scale changes had large impacts on global ecosystems, including those in the Pacific Northwest (Barnosky, 1984; Mathewes, 1991; Behl and Kennet, 1996; Hicock, et al., 1999; Lian et al., 2001; Thackray, 2001; Pisias et al. 2001; Grigg and Whitlock, 2002; Jiménez-Moreno et al., 2010; Harrison and Sanchez Goni, 2010).

Changes in the abundance and diversity of pollen and macrofossils in cores of lake sediments form the basis for much of our understanding of the LGM climate and ecosystems in the Pacific Northwest. Most of the sites studied to date are located in the southern Puget Lowland (Barnosky, 1981, 1985), coastal Olympic Peninsula (Heusser, 1974, 1978; Ashworth et al. 2021), Oregon (Grigg and Whitlock, 1998; Marshall et al. 2017), and British Columbia Fraser Lowland (Hicock and Lian, 1995; Telka et al., 2003; Hebda et al. 2016; Figs. 1 and 2). Research at these lowland sites has identified the basic pattern of plant geography and environmental change during the LGM, which is characterized by millennial-scale fluctuations between tundra and boreal (i.e., parkland, subalpine) vegetation (Heusser, 1977; Grigg and Whitlock, 2002; Lian et al., 2001; Ashworth et al., 2021). The variable LGM climate led to multiple advances of alpine glaciers in the Olympic and Cascade Mountains (Thackray, 2001; Porter and Swanson, 2008; Riedel et al., 2010; Whyshnytzky et al., 2019).

Major spatial and temporal gaps exist in the regional record, notably in the North Cascade Range in Washington State (Barnosky et al., 1987; Fig. 1). The limited number of sites investigated and poor age control limit regional correlations between sites and identification of the magnitude and timing of millennial-scale changes in climate (Jiménez-Moreno et al., 2010). Data for the early part of LGM are also scarce, particularly in areas like Skagit Valley that were subsequently covered by the Cordilleran ice sheet. Riedel (2007) described plant- and animal-rich macrofossil assemblages in well-exposed beds at two sites, 75 km apart, in Skagit Valley in the North Cascade Range (Fig. 1).

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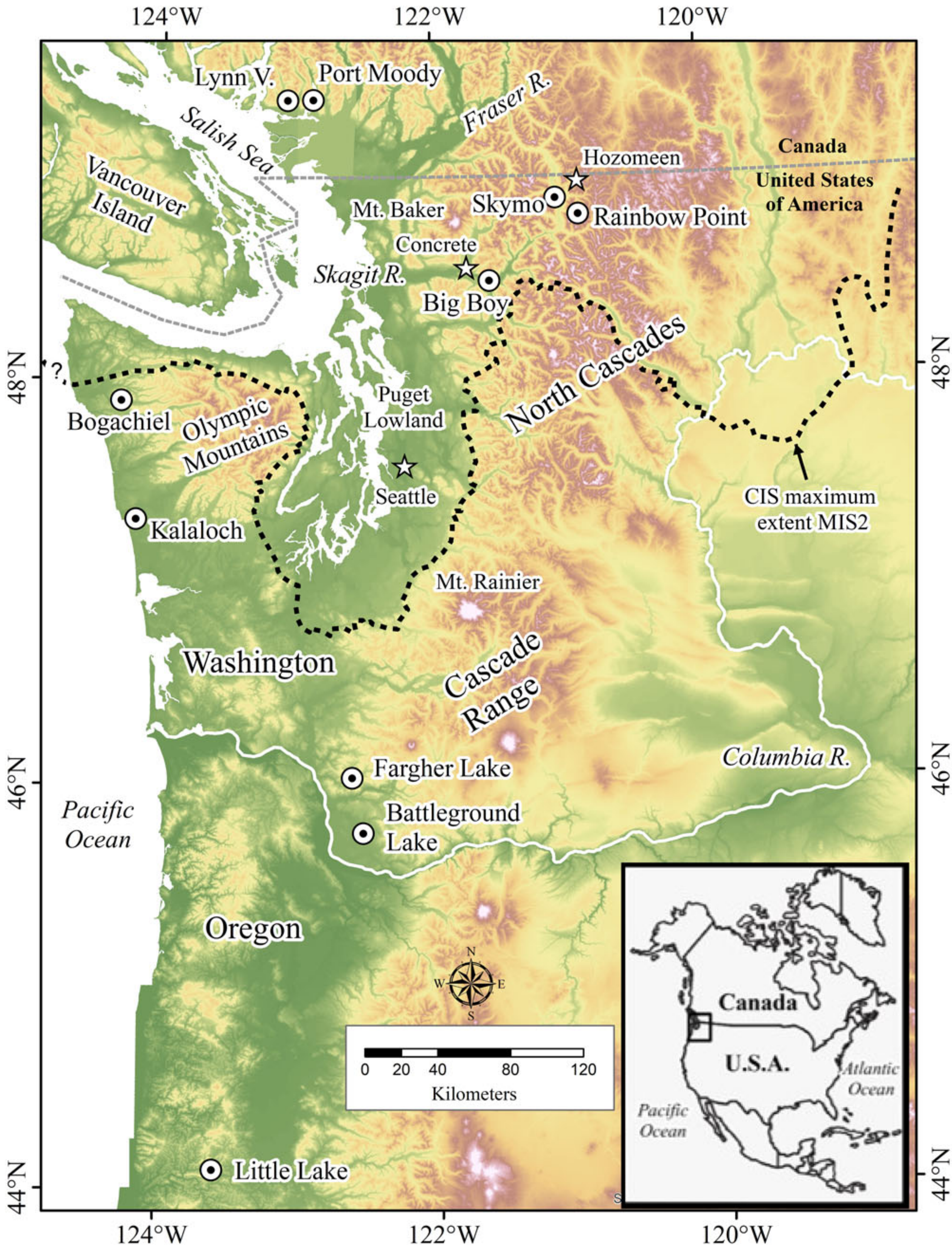

Figure 1. Paleoecological study sites dating to the last glacial maximum in western Washington and southwestern British Columbia (circles) and other place names referred to in the text (stars). Dashed line is Cordilleran ice sheet maximum extent during Marine Isotope Stage 2 (MIS 2) in Puget Lowland (Porter and Swanson, 1998) and the North Cascades (Waitt and Thorson, 1983; Riedel, 2017).

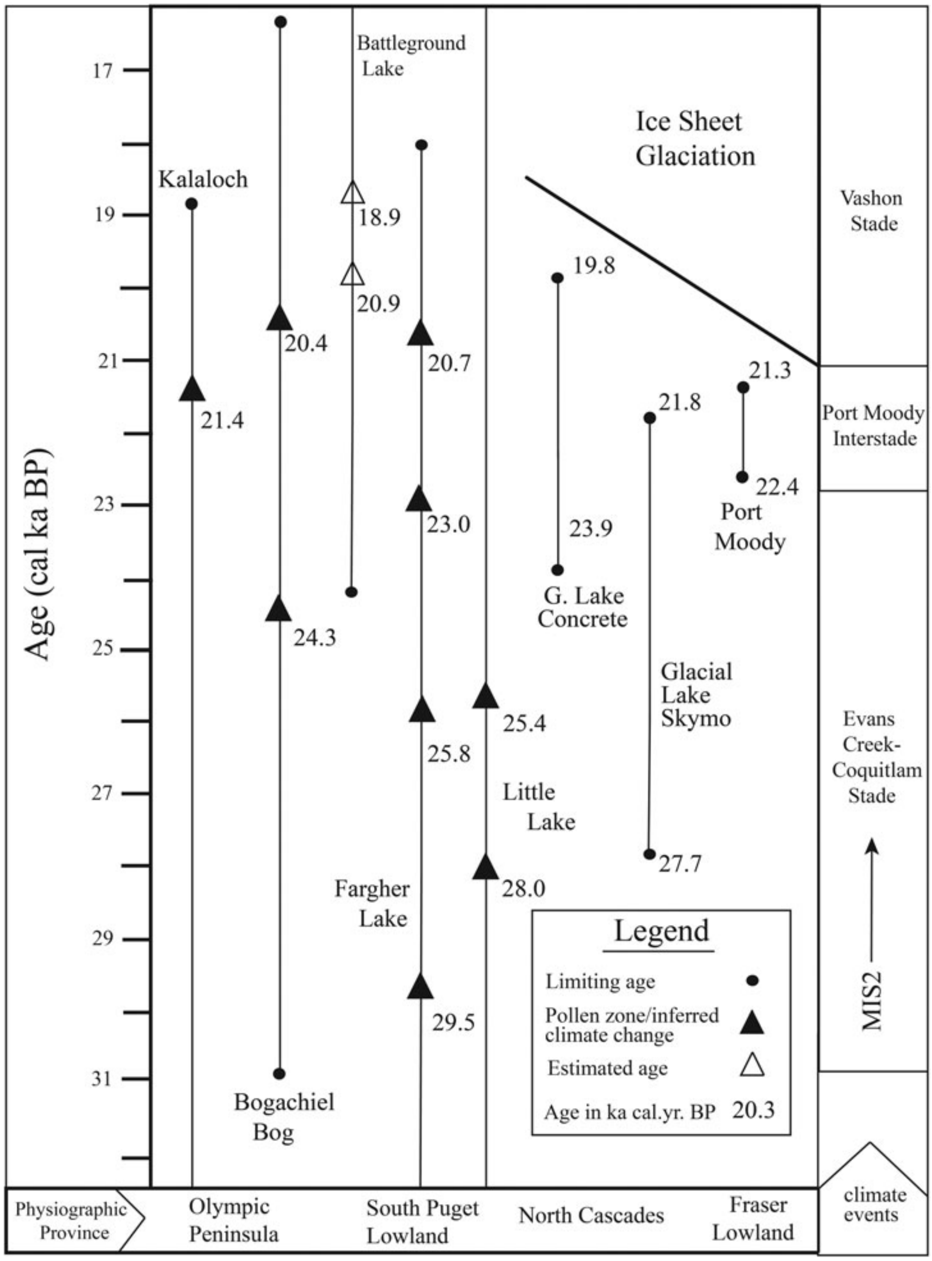

Figure 2. Last glacial maximum paleoenvironmental records from western Washington and southwestern British Columbia. Climate events on the right are after Armstrong et al. (1965) and Hicock and Lian (1995). Data sources: Bogachiel Bog: Heusser (1978); Hoh-Kalaloch: Heusser (1974, 1978, 1983) and Ashworth et al. (2021); Fargher Lake: Heusser and Heusser (1980) and Grigg and Whitlock (2002); Little Lake: Grigg et al. (2001) and Marshall et al. (2017); Battleground Lake: Barnosky (1981, 1985); Port Moody: Hicock and Armstrong (1981), Hicock et al. (1982), Hicock and Lian (1995), and Lian et al. (2001). MIS2, Marine Isotope Stage 2

This rich terrestrial record provided abundant material for radiocarbon dating and the potential to refine our understanding of the timing and magnitude of millennial-scale events in this region.

Our objective in this paper is to use the macrofossil assemblages from the Skagit Valley ice age refugia to describe the ecology of, and to quantitatively reconstruct climate during, the LGM. Macrofossils are excellent indicators of climate and provide context for understanding modern species distribution, adaptation, and evolution (Gavin et al., 2014). We use a probability density function (PDF) approach (Kühl et al., 2002) to estimate median annual precipitation (MAP) and July and January air temperatures at 12 times from 27.7 to 19.8 cal ka BP (all radiocarbon ages reported as thousands of calibrated years before present) based on the modern range and mean climate state of 14 species in the 12 macrofossil assemblages. The times and magnitudes of changes in precipitation and temperature are then used to identify millennial-scale climate variability. Finally, we compare the changes in the Skagit Valley record with regional and global changes in climate inferred from pollen records, ocean sediment cores, the activity of glaciers, and the chemistry of Greenland ice cores.

CLIMATE AND ECOLOGY OF SKAGIT VALLEY

The Skagit River watershed drains 8000 km^2 of rugged mountain topography with steep climate gradients and a wide range of

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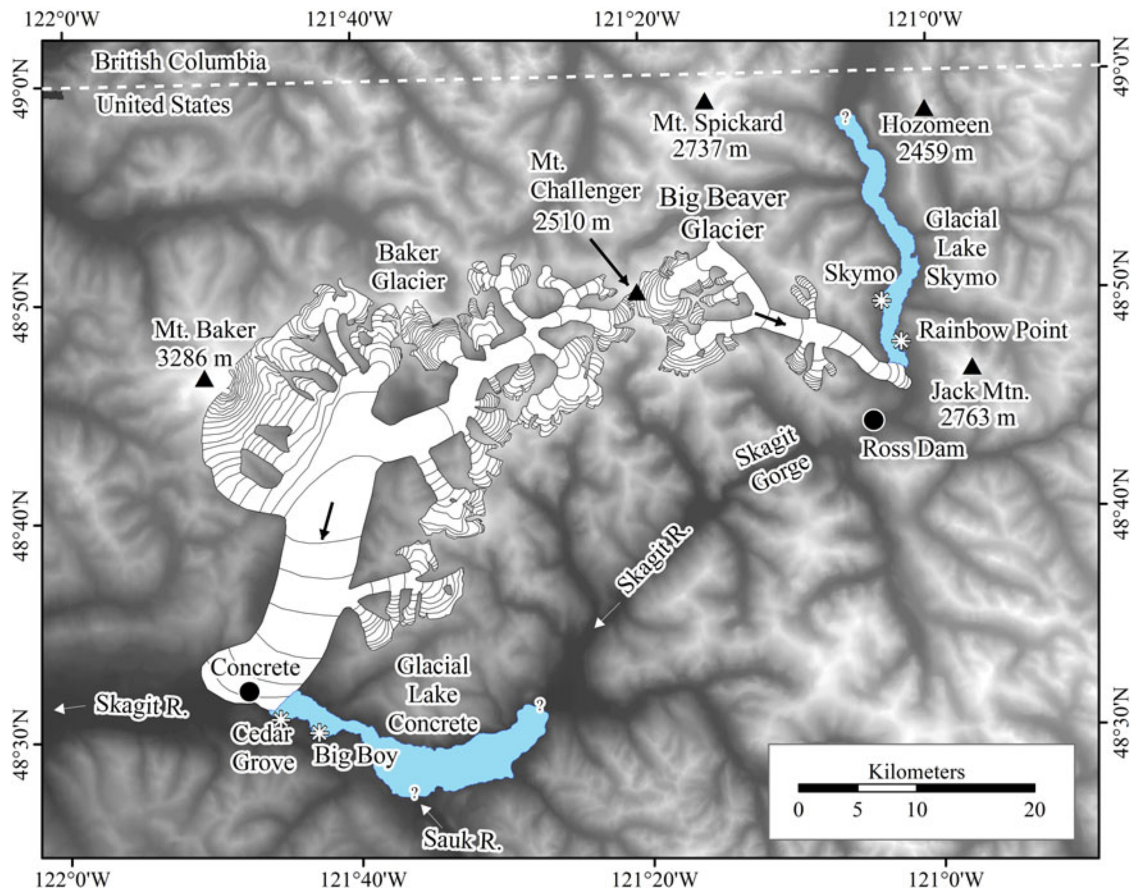

Figure 3. Extent of two alpine valley glacier systems and related lakes in Skagit Valley at the global last glacial maximum (Riedel et al., 2010). Alpine glaciers in adjacent valleys have not been reconstructed. Asterisks show locations of macrofossil beds reported in this paper.

physical and ecological conditions (Figs. 1 and 3). Fluvial and glacial erosion have cut a deep valley in metamorphic and granitic bedrock that dominates the catchment. Relief from the river delta to the summit of Mount Baker, the highest point in the watershed, is 3200 m (Fig. 1). The floor of Skagit Valley at Ross Lake, more than 150 km east of Puget Sound, is only 400 m above sea level (m asl). The valley shares several low-elevation divides with the Fraser River and Okanogan River watersheds due to elimination of geographic barriers by glacial breaching of mountain divides during continental glaciation (Flint, 1971; Riedel et al., 2007). For most of the Pleistocene, biota have been able to migrate into and out of Skagit Valley along the floors of these interconnected valleys, avoiding extreme conditions at higher elevations.

There are strong temperature and precipitation gradients with distance from Puget Sound and with elevation in Skagit Valley. Precipitation on the valley floor ranges from 1700 mm/yr at Concrete to 1000 mm/yr at Hozomeen Campground at the north end of Ross Lake (National Weather Service, 2019; Natural Resource Conservation Service, 2019; Fig. 1). There is a significant increase in the seasonal range of air temperature at Hozomeen due to the stronger continental climate and rain-shadow effect in upper Skagit Valley (Fig. 3). Mean annual precipitation increases significantly with elevation, and annual snowfall exceeds 20 m at higher elevations, feeding 377 glaciers in the Skagit River watershed (Riedel and Larrabee, 2016).

Mean July and January temperatures are 18.1°C and 2.5°C, respectively, on the floor of lower Skagit Valley at Concrete, and 18.8°C and −0.6°C at Hozomeen Campground in the upper valley (National Weather Service, 2019; Natural Resource Conservation Service, 2019; Fig. 1). The cool marine waters of Puget Sound suppress summer air temperatures and moderate winter air temperatures at Concrete. Seasonal climate variability is controlled now, as during the LGM, by the strength and position of the North Pacific High and the Aleutian Low (Oster et. al., 2015). The Aleutian Low strengthens and moves south in winter, bringing storms and a majority of the annual precipitation to western North America. In summer, the North Pacific high-pressure region moves north, creating dry weather.

Vegetation on the floor of lower Skagit Valley is currently dominated by temperate lowland forest conifers, including red cedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), and western hemlock (*Tsuga heterophylla*). Lowland trees also occupy the valley floor near Ross Lake, but xeric species such as ponderosa pine (*Pinus ponderosa*) are present on drier sites on the east side of the valley. Strong temperature and precipitation gradients control the elevation of the tree line and the distribution of tree-line species. In the western part of the watershed, the tree line is 1400 ± 150 m asl and is depressed by heavy winter snowfall (Franklin and Dyrness, 1988). Subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*) dominate the heavy snow and cool summer environments at the tree line in those areas. The tree line rises to 1700 ±150 m asl in the colder and more arid environment on the east side of Ross Lake near Hozomeen (Arno and Hammerly, 1984), where Engelmann spruce (*Picea engelmannii*) and whitebark pine (*Pinus albicaulis*) are the dominant subalpine species.

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Little information is available on contemporary beetle (Coleoptera) communities in Skagit Valley, although a survey of Big Beaver valley near Ross Lake yielded 360 species of terrestrial and aquatic beetles in 49 families (LaBonte, 1998), and Campbell (1983, 1984) conducted surveys of beetles near Mount Baker and in Manning Provincial Park in southwestern British Columbia. Data from these studies helped define the range of several key beetle species that are used in our quantitative analyses.

During the last Pleistocene glaciation (Fraser Glaciation, Marine Isotope Stage 2 [MIS 2]), glacial Lake Skymo (GLS) extended across the entire 2 km width of upper Skagit Valley over a distance of at least 15 km from a moraine or ice dam at the mouth of Big Beaver Creek (Riedel et al., 2010; Fig. 3). At about the same time and 75 km to the southwest and 400 m lower in elevation, glacial Lake Concrete (GLC) occupied a part of lower Skagit Valley (Fig. 3). The elevation of GLC (60 m asl) is similar to that of several other latest Pleistocene paleoecological sites in the region (Fig. 1). The elevation of GLS sediments is about 460 m asl, similar to elevations of the previously studied Fargher and Battleground lakes paleoecological sites (Fig. 1). However, GLS is farther east, deep in the Cascade Range, unlike any other previously reported site in Washington.

The glacial lake record at the LGM is fragmentary, because the 1800-m-thick, fast-advancing Cordilleran ice sheet buried or eroded most deposits (Riedel, 2017). However, lake sediments containing macrofossils are preserved down-ice of bedrock valley spurs in gullies 40 m above the valley floor along the shores of Ross Lake reservoir. These sediments are exposed by wave erosion during seasonal fluctuations of the level of the reservoir. Macrofossils are also preserved near the terminus of the ice sheet in lower Skagit Valley, where they covered by advance outwash and till (Riedel, 2017). They are exposed in two large cutbanks on the south side of Skagit River near the community of Concrete (Fig. 3). Both lakes trapped and preserved macrofossils in silt, because they had stable bedrock outlets that maintained relatively consistent water surface levels and shorelines (Riedel et al., 2010). The lakes had maximum depths of 40 m (GLC) and 80 m (GLS) (Riedel et al., 2010; Fig. 3).

METHODS

Data sources

We obtained bulk sediment samples from three sections in Skagit Valley: two along the shoreline of Ross Lake and one along Skagit River near Concrete (Riedel, 2007; Riedel et al. 2010; Fig. 3). The organic content of each sample was measured by volume after removing detrital sediment (Supplementary Material 1). We focused on macrofossils from these sites because they are abundant in accessible, well-exposed beds and, unlike most coniferous pollen, can be identified to the species level.

We collected 1 and 2 L samples from 12 glaciolacustrine beds (Figs. 3 and 4). We collected most samples in a vertical sequence at each section, but in some cases, we moved laterally to sample because of limitations imposed by exposure and debris flow deposits. Beds were sampled at approximate 100–200 cm intervals at GLC and 200–400 cm at GLS. The sampling interval is roughly equivalent to 650 yr, a temporal resolution similar to most pollen studies (Whitlock, 1992). At this temporal scale, vegetation can respond to significant changes in climate (Birks and Birks, 1981).

The macrofossils were examined in detail at two laboratories: the Paleotech laboratory in Ottawa (all species) and the School of Environmental and Forest Sciences at the University of Washington in Seattle (conifers), where modern reference collections were used for identification. In three samples we looked only for conifer needles. In final needle counts, we used whole needles plus the number of tips and bases divided by two. Laboratory and identification procedures are summarized in Supplementary Material 1.

Riedel (2007) obtained radiocarbon ages on 10 of 12 assemblages to establish a chronological framework (Supplementary Material 5). We use linear depth–age models from both glacial lakes to infer the ages of two undated samples between dated beds and rounded those interpolated ages to the nearest 100 yr (Riedel et al., 2010). Accelerator mass spectrometry (AMS) ages were determined at Beta Analytic Laboratory, Lawrence Livermore National Laboratory, and the University of California Irvine Keck Carbon Cycle AMS Laboratory (Supplementary Material 5). We calibrated our raw radiocarbon ages and those previously published on regional pollen zone boundaries and glacial events using OxCal 4.3 (Bronk Ramsay, 2009; Supplementary Material 5). All calendric ages reported herein are the most probable (median) age, with a 2σ range (95.4%) provided on some figures and in the Supplementary Material.

We focus on 14 species of macrofossils to characterize the LGM climate of Skagit Valley (Table 1). We were unable to distinguish silver fir (*Abies amabilis*) from grand fir (*Abies grandis*) and Douglas-fir from western hemlock. Many of these species exist today in cold and dry boreal or alpine settings, although disjunct populations occur at lower elevations and latitudes in favorable microclimates. Like Barnosky (1984), we use mountain hemlock and Engelmann spruce as primary indicators of the Late Pleistocene climate in Puget Lowland because they are distributed at opposite ends of a maritime (cool/wet) to continental (cold/dry) subalpine climate transect at the tree line (Franklin and Dyrness, 1988; Mathewes, 1993). Whitebark pine occurs in cold dry climates at high elevations on the eastern slopes of the Cascade and Coast Mountains (Franklin and Dyrness, 1988; Lian et al., 2001). Northern spikemoss (*Selaginella selaginoides*) and black crowberry heath (*Empetrum nigrum*) live today in coastal settings from northern Vancouver Island north to Alaska (Franklin and Dyrness, 1988; Heusser and Igarashi, 1994). Heusser and Peteet (1988) used northern spikemoss in paleoecological reconstructions along the Pacific coast to identify open boreal conditions.

We use three beetle species in the Staphylinidae family as climate indicators (Table 1). The predatory rove beetles *Eunecosum tenue*, *Olophrum consimile*, and *Olophrum boreale* are thought to respond rapidly to climate change (Elias, 2002; Ashworth et al., 2021). All three species have relatively narrow temperature tolerances and are found today in northern boreal, subarctic, and alpine settings in cool moist habitats along streams and lakeshores (Campbell, 1983, 1984; Elias, 2002). *Olophrum consimile* prefers more maritime environments, whereas *O. boreale* is found in more continental settings. Disjunct populations of these species have been found in alpine and subalpine settings near Skagit Valley. *Olophrum consimile* was identified in the modern Big Beaver study near Ross Lake and at Austin Pass near Mount Baker (LaBonte, 1998).

We obtained modern range maps for trees from the Climate Vegetation Atlas (Thompson et al., 2015) and range data for beetles from Campbell (1983, 1984) and A. Ashworth (written communication, 2018). We use gridded climate data to develop the July, January, and annual precipitation probability distributions

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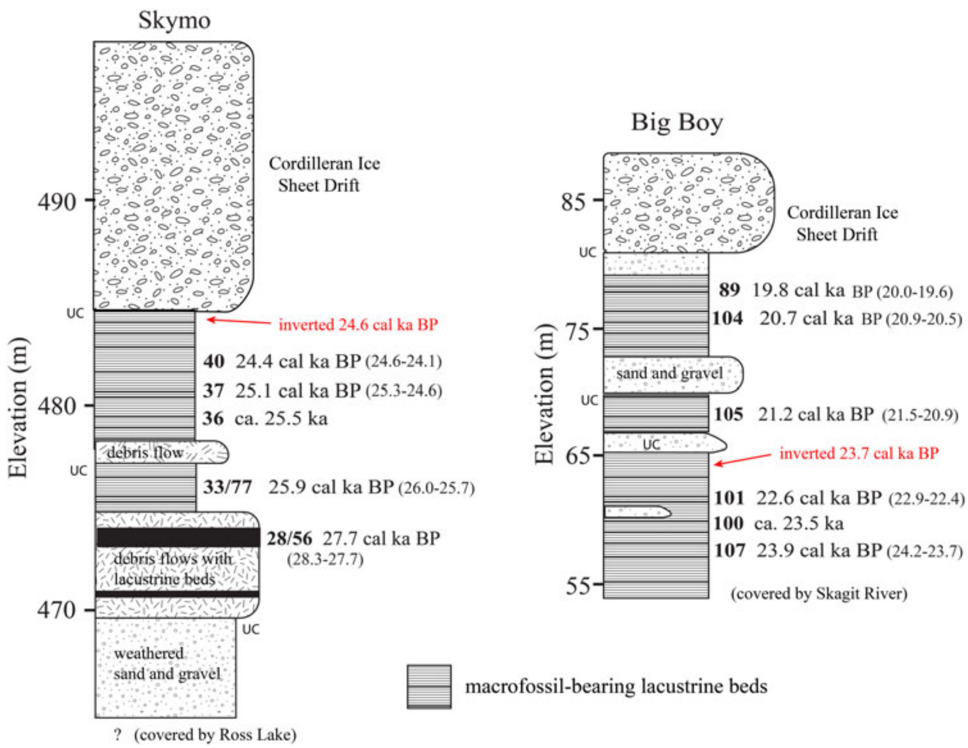

Figure 4. Key Skagit Valley stratigraphic sections showing approximate last glacial maximum assemblage locations and associated median radiocarbon ages in cal ka BP (2σ age range in parentheses). Unconformable contacts marked by "UC." Note: Ages differ slightly from those in Riedel et al. (2010) due to the use of different calibration programs.

for each indicator species (Wang et al., 2012). These data are based on PRISM (Parameter Elevation Regression on Independent Slopes Model), a method that interpolates 30-yr normal climate observations (1981–2010) across complex topography with 4 km resolution.

Data analysis

We use the PDF method of Kühl et al. (2002) to make quantitative climate estimates from the macrofossil assemblages. All analyses were completed in R and C code v. 3.53 provided by Kühl (Aarnes et al., 2012; R Core Team, 2019). This approach uses species presence/absence with modern range and climate data to develop probabilistic envelopes of one or more climate variables (Aarnes et al., 2012; Fig. 5). The PDF approach integrates conditional PDFs for all species present at a given time to generate estimates of climate for an assemblage of those species. This method reduces the dependence of climate estimates on single species that have wide climate envelopes. We focus on median values of annual precipitation and July and January air temperatures. We do not report mean values, because PDF distributions are not normal, making the median value a better measure of central tendency.

We considered abundance and diversity of all species to confirm PDF results of climate variability (Table 2). We compare our PDF results with regional pollen, ocean sediment cores, and glacial geology records to confirm the magnitude of climate changes and the timing of millennial-scale variability (Heusser, 1977; Barnosky, 1985; Clark and Bartlein, 1995; Hicock et al., 1999; Pisias et al., 2001; Thackray, 2001; Grigg and Whitlock, 2002; Jiménez-Moreno et al., 2010; Riedel et al., 2010; Fig. 2). Finally, we compare the Skagit-enhanced regional paleoclimate history to the oxygen-isotope record in the NRGIP GICCO5 chronology (Svensson et al., 2008) and the stades and interstades identified in these records (Harrison and Sanchez Goni, 2010).

Sources of error

Our temporally coarse sample scheme and 1–2 L sample size limit the influence of needle production rate on our results (Birks and Birks, 1981). Based on the relatively slow sedimentation rates of 4–5 mm/yr in GLC and GLS (Riedel et al., 2010), each sample should span more than 50 yr, thereby reducing the effect of variability in needle production between species and the influence of short-term disturbance events and seasonal variation in needle production.

The main sources of error in our analysis include sampling, potential mixing of specimens between beds, and limitations of the PDF approach. We attempted to assure the integrity of macrofossil samples by collecting them from undisturbed beds of laminated silt and clay. Well-preserved specimens, including articulated beetles, and the preponderance of radiocarbon ages in stratigraphic order also indicate that disturbance was not continuous.

Taphonomic processes that lead to macrofossil deposition include redistribution by currents and wind. In GLC and GLS, these processes may have affected macrofossil abundance and diversity in individual samples. This is clearly shown by the general lack of macrofossils in GLS beds on the east side of Skagit Valley, whereas some samples collected on the west shore 2.5 km across the valley contain thousands of macrofossils. We assume that taphonomic factors that might cause differential sorting of needles were constant through time for samples collected vertically in a section at a given site. However, inverted radiocarbon ages at the main sample sites indicate that some mixing of

Table 1. Indicator plant and insect macrofossils and their modern climate means fro Climate WNA (Wang et al. 2012) derived from range data for trees from Thompson et al. (2015) and beetles from A. Ashworth (written communication, 2018).

Species	Mean July (°C)	Mean January (°C)	Mean annual precipitation (mm)	Modern megabiome[a]	High-elevation equivalent[b]
Probability density function indicator species					
Abies amabilis	13.3	−2.5	2711	Temperate forest	Montane/TRF
Abies grandis	16.1	−1.3	1566	Temperate forest	Montane/TRF
Abies lasiocarpa	15.0	−11.7	869	Boreal	Subalpine
Abies procera	16.0	−0.2	1974	Temperate forest	Montane forest
Betula nana	13.5	−18.5	565	Boreal/subarctic	Subalpine/alpine
Picea engelmannii	14.1	−7.9	890	Boreal	Subalpine/dry
Picea sitchensis	13.5	−2.7	2828	Temperate forest	TRF
Pinus albicaulis	12.7	−8.2	1177	Boreal	Subalpine/dry
Pseudotsuga menziesii	15.7	−4.0	1116	Temperate forest	Temperate forest
Tsuga heterophylla	13.5	−3.8	2366	Temperate forest	Temperate forest
Tsuga mertensiana	12.8	−4.4	2720	Boreal	Subalpine/wet
Eucnecosum tenue	12.1	−16.3	901	Boreal	Subalpine
Olophrum boreale	12.5	−19.5	663	Boreal	Subalpine
Olophrum consimile	15.1	−12.9	909	Boreal	Subalpine
Other species[c]					
Empetrum nigrum	12.8	−20.5	567	Boreal/subarctic	Subalpine/alpine
Juncus bufonius	17.0	−1.9	799	Temperate forest	TRF
Potamogeton alpinus	15.8	−14.3	677	Boreal	Subalpine
Potentilla anserina	15.8	−10.0	717	Temperate forest	TRF
Rubus idaeus	17.4	−11.4	729	Temperate forest	TRF
Selaginella selaginoides	14.2	−18.2	637	Boreal	Subalpine
Stuckenia vaginata	15.5	−16.2	575	Boreal	Subalpine
Modern climate[d]					
Concrete, Washington (1925–2018)	18.1	2.5	1700	Temperate forest	Temperate forest
Hozomeen, Washington (2001–2018)	18.8	−0.6	1000	Temperate forest	Temperate forest

[a]Megabiomes and related high-elevation terms from Jiménez-Moreno et al. (2010).
[b]TRF, temperate rain forest.
[c]Climate and range of other species from the WorldClim data set (Fick and Hijmans, 2017) and version 4.1 of the Botanical Information and Ecology Network (Enquist et al., 2016), respectively.
[d]Modern climate in Skagit Valley from National Weather Service (2019) for Concrete and Natural Resource Conservation Service (2019) for Hozomeen.

specimens from older beds into younger ones may have occurred in both glacial lakes.

The primary sources of uncertainty in the PDF method are the wide ecological range of some species and a low number of species identified in some assemblages. The presence of three or fewer species in 5 of the 12 assemblages is the most significant source of error in this analysis. Aarnes et al. (2012) used a similar approach that had several samples with fewer than three species. They urged caution when interpreting results from small samples but found that removing them from their analysis had a small effect on the overall climate estimate. The uncertainty in each PDF estimate is the result of the uncertainty in each of the species estimates. The error in the estimate of average climate over the period of record is the average of the error from each assemblage used ($n > 3$; Table 3). Our reliance on tree macrofossils increases uncertainty in our results, because many of the species have broad ecological ranges (Table 1). Accuracy of the Thompson et al. (2015) range maps and the inherent compromises made when producing a gridded climate product like PRISM are other potential sources of error. We did not conduct a modern calibration test.

RESULTS

Macrofossil-bearing glacial lake sediments from the two sites in Skagit Valley span nearly 8000 yr during the LGM (early MIS 2). The GLS beds range from 27.7 to 21.8 cal ka BP, and the GLC beds from 23.9 to 19.8 cal ka BP (Figs. 3 and 4). Riedel et al. (2010) described the stratigraphy, sedimentology, and geochronology at these sites. We provide a brief summary of the biological component of each assemblage here; more detailed descriptions and radiocarbon age data are presented in the Supplementary Material.

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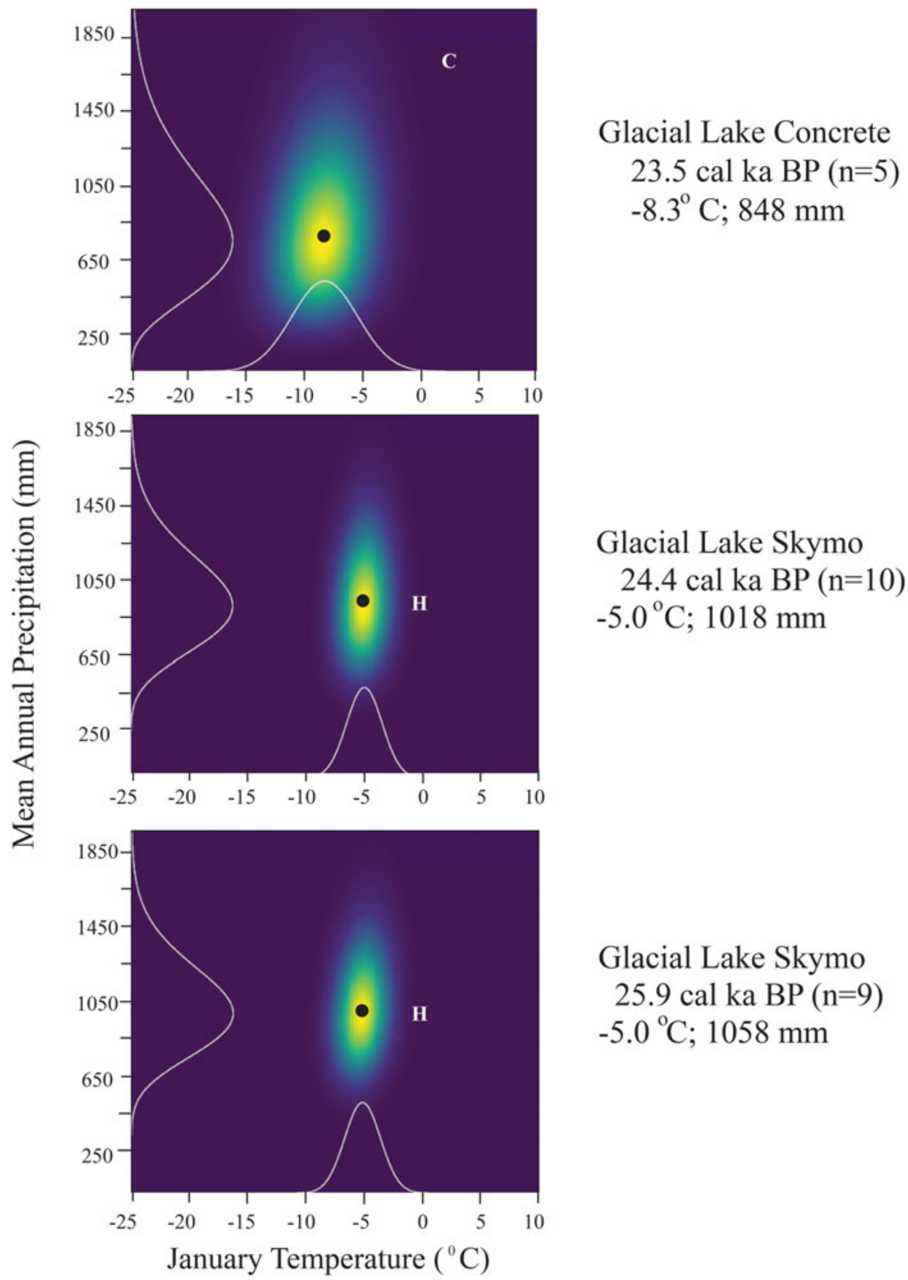

Figure 5. Probability density function plots of mean annual precipitation and mean January air temperature for three time periods based on the Skagit glacial lake macrofossil assemblages. Warmer colors indicate higher probability; white lines show scaled probability distributions; and black dots most probable value (median). Modern climate shown for reference at Concrete (C) and Hozomeen (H).

An inverted radiocarbon age was obtained from a bed directly below ice sheet till but several meters above sample NOCA 40 at GLS (Riedel et al., 2010; Fig. 4). One inverted radiocarbon age from GLC was obtained from beneath an alluvial gravel deposit unconformably overlying the lake beds (Fig. 4). The inverted age was from a bed about 50 cm above NOCA 101 (Fig. 4; Supplementary Material 4).

Glacial Lake Skymo

We recovered macrofossils at the Skymo and Rainbow Point sections along the shoreline of Ross Lake in upper Skagit Valley (Figs. 3 and 4). Most of the plant macrofossils and all the faunal remains came from the Skymo section on the west shore of the former glacial lake. The abundance of macrofossils at the Skymo section and their rarity at Rainbow Point suggests they were concentrated in bays on the west side of the lake by easterly winds. Only a few conifer needles were found near the top and bottom of the Rainbow Point section, but they extend the GLS record by 2600 yr (Fig. 6).

Some of the GLS samples contain few macrofossils, whereas others have thousands of specimens (Fig. 6; Supplementary Material 2). The oldest sample at GLS, collected from the Rainbow Point section, dates to 27.7 cal ka BP (NOCA 28/56) and includes needle tips and bases from three tree species: Douglas-fir/western hemlock, mountain hemlock, and Engelmann spruce.

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Table 2. Summary of glacial Lake Concrete (GLC) and glacial Lake Skymo (GLS) macrofossil assemblages.

Sample	Age (cal ka BP)	Organic content (% by volume)[a]	Number of taxa
GLC			
NOCA 89	19.8	N/A	2
NOCA 104	20.7	39	30
NOCA 105	21.2	40	39
NOCA 101	22.7	100	17
NOCA 100	23.5	43	22
NOCA 107	23.9	N/A	2
GLS			
NOCA 61/98	21.8	N/A	5
NOCA 40	24.4	17	32
NOCA 37	25.1	25	25
NOCA 36	25.5	<1	2
NOCA 33/77	25.9	16	24
NOCA 56/28	27.7	N/A	4

[a]N/A, no measurement of total organic content; conifer needle counts only.

The next sample in the sequence, from the Skymo section (NOCA 33/77), yielded an age of 25.9 cal ka BP and is rich in plant macrofossils, with 24 taxa (Table 2). The assemblage is dominated by needles of subalpine fir, Engelmann spruce, and whitebark pine (Fig. 6). It also includes boreal/subarctic nutlets of dwarf birch (*Betula nana*) and black crowberry heath (see photo Supplementary Material 3). This assemblage contains weevils (Curculionidae) and bark (Scolytidae), rove (Staphylinidae), and pill (Byrrhidae) beetles (Supplementary Material 4). Sample NOCA 36 at 25.5 cal ka BP contains less than 1% organic material by volume and only a few subalpine tree macrofossils (it was not examined for non-conifer species).

Sample NOCA 37 (25.1 cal ka BP) contains 25 taxa (Table 2). Whitebark pine is the dominant species, with hundreds of needles and many fascicles, followed by sedge (*Carex*) achenes. The assemblage also includes needles of the temperate/montane species grand/silver fir, several species of rove and bark beetles, and two unknown genera of weevils.

Sample NOCA 40 (24.4 cal ka BP), with 17% organic material, is taxonomically the richest at the Skymo section, with 32 taxa. Subalpine trees are dominant, but the assemblage includes temperate forest species (Fig. 6). We also found the cold-adapted rove beetles (Staphylinidae) *Eucnecosum tenue* and *Olophrum boreale*, as well as bark and ground beetles (Carabidae) in this sample.

Two samples collected at the Rainbow Point section on the east shore of Ross Lake (NOCA 61 and 98) yielded 21 coniferous macrofossils that could be identified to the species level (Fig. 6). They include Engelmann spruce, mountain hemlock, subalpine fir, and four needles of either western hemlock or Douglas-fir (Fig. 6; Supplementary Material 3).

The cold waters of GLS also sustained several aquatic flora and fauna. Samples NOCA 37 and 40 contain the circumboreal pondweed (*Potamogeton alpinus*), and samples NOCA 33, 37, and 40 contain the emergent white water buttercup (*Ranunculus aquatilus*). The lake was also inhabited by predaceous diving beetles (Dystiscidae), water scavenger beetles (Hydrophilidae), caddisflies, water fleas, and midges (Chironomidae) (Supplementary Material 4).

Glacial Lake Concrete

The 29-m-tall Big Boy section on the south bank of Skagit River provides access to the well-exposed lacustrine sediments (Riedel et al., 2010; Fig. 4). We examined the lowest sample NOCA 107 (23.9 cal ka BP) for conifer needles and found only two, grand/silver fir and subalpine fir.

The next sample in the sequence (NOCA 100; 23.5 cal ka BP) yielded 22 taxa, including two boreal beetles (the rove beetle *O. boreale* and the ground beetle *Elaphrus clairvillei)* and northern spikemoss (Fig. 7; Supplementary Material). The assemblage contained subalpine fir, Engelmann spruce and Sitka spruce needles (*Picea sitchensis*; Fig. 6).

Sample NOCA 101 (22.7 cal ka BP) contains 17 taxa, including abundant sedge achenes and northern spikemoss megaspores identified on the basis of large spore size (0.48–0.53 mm) and yellow-green color (Tyron, 1949; Fig. 6; Table 2). Northern spikemoss macrofossils have not previously been found in Pleistocene sediments in the Cascade Range (Heusser and Igarashi, 1994). The boreal beetles *E. clairvillei* and *O. consimile* are also present in the assemblage. Sample NOCA 101 contains two groups not found lower in the section: feather-wing beetles (Ptiliidae) and click beetles (Elateridae) (Supplementary Material 4).

Sample NOCA 105 (21.2 cal ka BP) was collected from a dark-gray silt bed consisting of 40% organic material, three-quarters of which is moss and most of the remainder flattened twigs, bark, and horsetail (*Equisetum*) fragments (Table 2). It is the richest GLC assemblage, with 39 taxa, including silver fir and subalpine fir needles, along with many sedge achenes, nearly 70% of which have partial seed coats. The second most common macrofossils are willow (*Salix*) seed capsules, twigs, and persistent buds. The sample also contains several other taxa that were not found lower in the section, including rush (*Luzula* and Juncaceae spp.) seeds, buckwheat (*Polygonum* sp.), and silverweed cinquefoil (*Potentilla anserina*; Supplementary Material 3). The assemblage includes two species of ground beetles (Carabidae); nine species of rove beetles, including oscellate species *O. consimile* and *O. boreale*; click beetles (Ptiliidae); leaf beetles (Chrysomelidae); and weevils (Curculionidae). It also includes several species of aquatic beetles.

Sample NOCA 104 (20.7 cal ka BP), collected from near the top of the Big Boy lacustirine sequence, contains 30 taxa dominated by subalpine fir and Engelmann spruce needles (Fig. 6; Table 2). Notably absent from the assemblage are northern spikemoss macrofossils, which are abundant lower in the section. A complete, flattened Engelmann spruce cone (NOCA 89; 19.8 cal ka BP) is the youngest dated macrofossil at the Big Boy section and was identified based on cone length and diameter. The NOCA 104 assemblage contains fewer species of beetles than NOCA 105, but still is a diverse collection of ground, rove, click, and leaf beetles. It also includes weevils, pill beetles (Elateridae), and two species of dung beetles (Scarabaeidae), but no aquatic taxa (Supplementary Material 4).

Paleoclimate

The PDF analysis relies on 14 species that are present at 12 times during the LGM at the two glacial lakes (Figs. 5 and 7; Table 3).

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Table 3. Results of the probability density function reconstruction of climate in Skagit Valley during the last glacial maximum.

Age (cal ka BP)	No. of species	Median Jan. (°C)	1σ SD (°C)	Median July (°C)	1σ SD (°C)	Median annual precipitation (mm)	1σ SD (mm)
Glacial Lake Skymo (GLS)							
21.8	5	−6.2	±2.4	14.6	±1.8	822	±332
24.4	10	−5.0	±1.5	14.1	±1.2	1018	±257
25.1	5	−9.3	±2.3	12.6	±1.7	848	±258
25.5	2	−8.8	±3.4	13.9	±2.9	704	±376
25.9	9	−5.0	±1.5	13.9	±1.2	1058	±241
27.7	3	−6.4	±2.9	14.4	±2.3	901	±406
GLS $n > 3$ average		−6.8	±1.9	12.5	±1.5	937	±272
Modern		−0.6		18.8		1000	
Glacial Lake Concrete (GLC)							
19.8	1	−7.9	±4.1	14.4	±4.0	783	±454
20.7	5	−6.2	±2.6	14.6	±1.8	848	±336
21.2	4	−7.6	±4.4	14.6	±2.4	809	±384
22.7	3	−8.1	±3.5	14.6	±3.2	575	±376
23.5	5	−8.3	±2.9	13.1	±2.0	848	±341
23.9	2	−6.2	±4.9	14.7	±2.8	874	±454
GLC $n > 3$ average		−7.4	±3.3	13.9	±2.1	835	±354
Modern		2.5		18.1		1700	

Climate reconstructions for seven assemblages are based on four to nine species, whereas the other five are limited to one to three species (Fig. 6; Table 3). The resulting large errors in the climate estimates for the five assemblages are unavoidable, because we could not include aquatic species or those without reliable range information (Fig. 7; Tables 1 and 3). However, the PDF procedure is insensitive to the removal of some groups, including beetles and some plant species with broad environmental ranges (Table 1).

We averaged the PDF climate estimates at each site for all assemblages with more than three species to get a broad estimate of climate change during the entire LGM (Table 3). At GLS, median January and July air temperatures were −6.8 ± 1.9°C and 12.5 ±1.5°C, respectively, and MAP was 937 ± 272 mm (Table 3). The corresponding averages at GLC were −7.4 ± 3.3°C, 13.9 ± 2.1°C, and 835 ± 354 mm, respectively.

All our PDF climate estimates represent large changes from today's climate in Skagit Valley. Average median July air temperature for all assemblages was 4.2°C lower than today at GLC and 6.3°C lower than today at GLS (Fig. 7). Average median January air temperature was depressed more at GLC (−9.9°C) than at GLS (−6.2°C; Fig. 7). Mean annual precipitation also changed more at GLC, with a decrease of 50% compared with 10% in the more continental environment at GLS.

Our PDF results reveal variations in all three climate indices during the LGM (Fig. 7; Table 3). Median January air temperature fluctuated ±4.3°C at GLS and ±2.1°C at GLC (Table 3). Median July air temperature varied ±2.0°C at GLS and ±1.6°C at GLC. MAP ranged from 822 ± 332 to 1058 ± 241 mm at GLS and from 575 ± 376 to 874 ± 454 mm at GLC. The PDF results show a slight drying trend from 25.9 to 21.7 cal ka BP at GLS (Fig. 7). Climate variability is indicated by warmer winters and higher precipitation at 27.7, 25.9, and 24.4 cal ka BP at GLS, and from 21.2 cal ka BP until at least 20.7 cal ka BP at GLC (Fig. 7).

DISCUSSION

LGM paleoecology

We cannot rule out mixing of macrofossils from higher elevations, particularly in upper Skagit Valley, where the waters of GLS intersected steep slopes. However, the large number of subalpine macrofossils and fossil preservation suggest they were not transported far by slope or alluvial processes. We infer that differing microclimates along the lake shorelines were the main factor allowing both temperate forest and open boreal species to share the same habitat during certain periods. Microclimates existed due to elevation, topographic shading/exposure, cold air drainage down tributary valleys, and abundant moisture along the lakes. They exist today as illustrated by the presence of disjunct populations of ponderosa pine, aspen (*Populus*), and juniper (*Juniperus*) on the east shore of Ross Lake.

The different settings of GLS and GLC are responsible for clear differences in plant and insect assemblages. GLC beds are about 50 m asl, whereas GLS beds, 75 km to the east, are 400 m higher and in the rain shadow of the Picket Range. The lower elevation and wider valley setting at GLC are likely responsible for its higher floral and faunal diversity. Early in the GLC record, there were few conifers and abundant wetland species, including willow, mosses, and sedges. Most of the insects, including beetles, are aquatic and semiaquatic; no bark beetles are present. In contrast, GLS assemblages contain three species of cold-adapted bark

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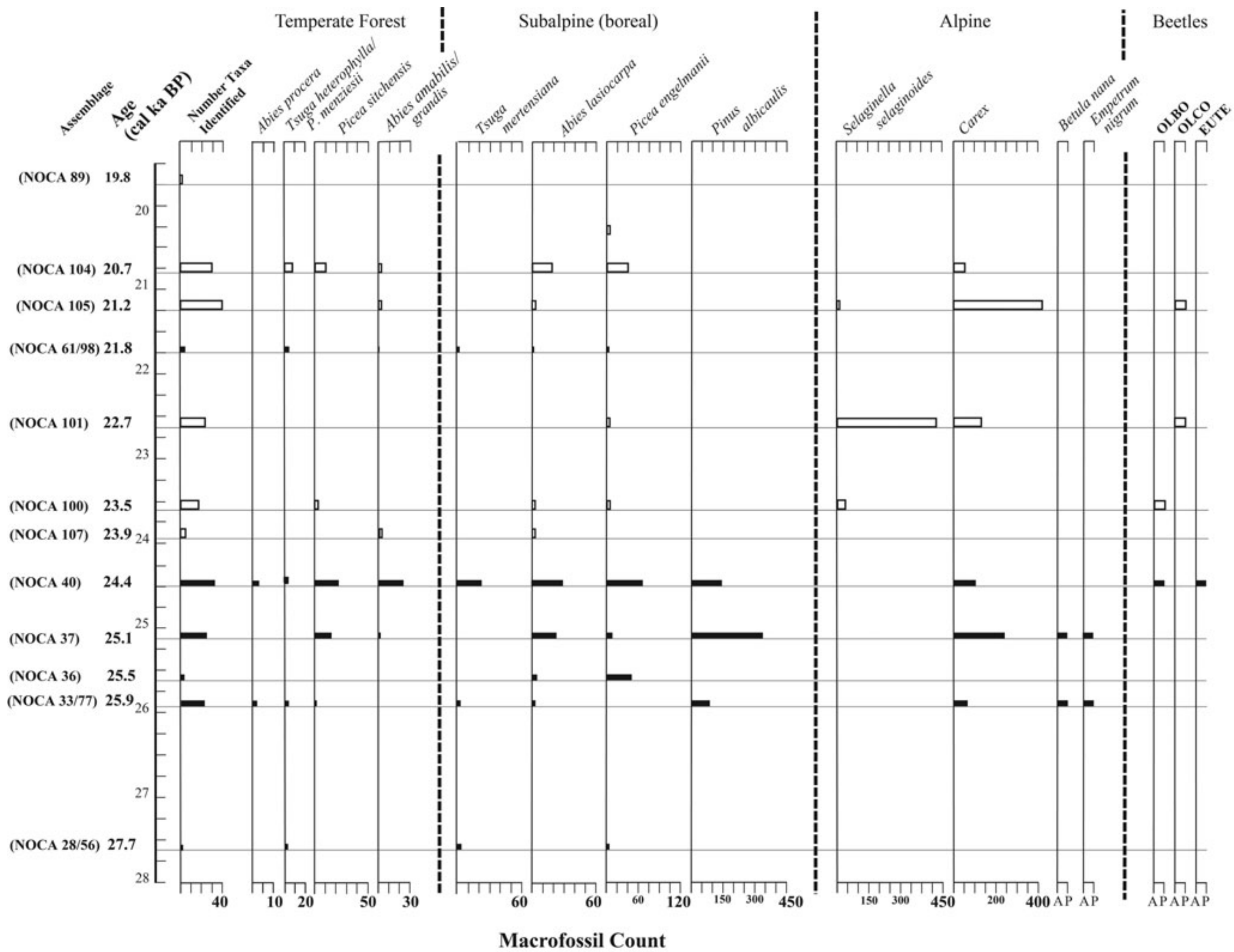

Figure 6. Macrofossil diversity and abundance through time ing Lake Concrete (open bars) and glacial Lake Skymo (black bars) assemblages. The species shown are those used in the probability density function analysis and others of interest. Note change in scale for abundant species (e.g., *Picea engelmanii*, *Pinus albicaulis*, *Selaginella selagenoides*, and *Carex*), and the change to presence (P)/absence (A) for rare boreal species and beetles (*Olophrum boreae* [OLBO], *Olophrum consimile* [OLCO], and *Eucnecosum tenue* [EUTE]).

beetles, open boreal plants, and abundant arid subalpine tree macrofossils (Supplementary Material 4).

The temperate forest, montane, subalpine (boreal), and alpine (subarctic) species in the Skagit assemblages are found today at different latitudes, elevations, and distances from the moderating influence of the Pacific Ocean. Several of the assemblages contain temperate forest species and open boreal shrubs, mosses, and beetles. Full-glacial plant communities in the Pacific Northwest typically do not have modern analogs (Heusser, 1974, 1977; Barnosky, 1981; Whitlock, 1992; Lian et al., 2001).

Thousands of macrofossils of Engelmann spruce, whitebark pine, and subalpine fir dominate the Skagit Valley assemblages. They record a dry subalpine forest biome in a cold, dry continental climate during the LGM (Table 1). These trees currently grow near the tree line at elevations 1200 m above the GLS beds on the east side of the valley and at lower elevations near the heads of dry cold valleys (Arno and Hammerly, 1984).

Assemblages from both glacial lakes provide clear evidence of open boreal (subalpine) conditions at various times. Cold-adapted species present in the Skagit Valley assemblages include alpine pondweed, dwarf birch, black crowberry heath, northern spikemoss, the ground beetle *E. clairvillei*, and the rove beetles *O. boreale* and *E. tenue* (Table 1; Supplementary Material 4). All of these species are common today in boreal forests and at higher elevations in the Rocky Mountains (Campbell, 1984; Ashworth et al., 2021). *Olophrum boreale*, *O. consimile, and E. clairvillei* were found in Late Pleistocene beds at Kalaloch on Olympic Peninsula and in Seattle (Cong and Ashworth, 1996; Ashworth and Nelson, 2014; Ashworth et al., 2021).

Northern spikemoss megaspores are abundant in the early part of the GLC record. One liter of sediment dated at 22.7 cal ka BP yielded 462 megaspores (Fig. 6; Supplementary Material 2 and 3). Northern spikemoss is typically associated with open nonarboreal environments and requires a cool stable habitat and a high water table (Heusser and Peteet, 1988; Heusser and Igarashi, 1994). Western Washington is currently outside its range (Heusser and Peteet, 1988), but northern spikemoss occurs on northern Vancouver Island and in coastal British Columbia and Alaska (Heusser and Igarashi, 1994). It also is present in the Rocky Mountains of Idaho, Wyoming, and Montana, where it grows above 2085 m asl in association with willow thickets in open meadows and along ponds and streams (Scoggan, 1978).

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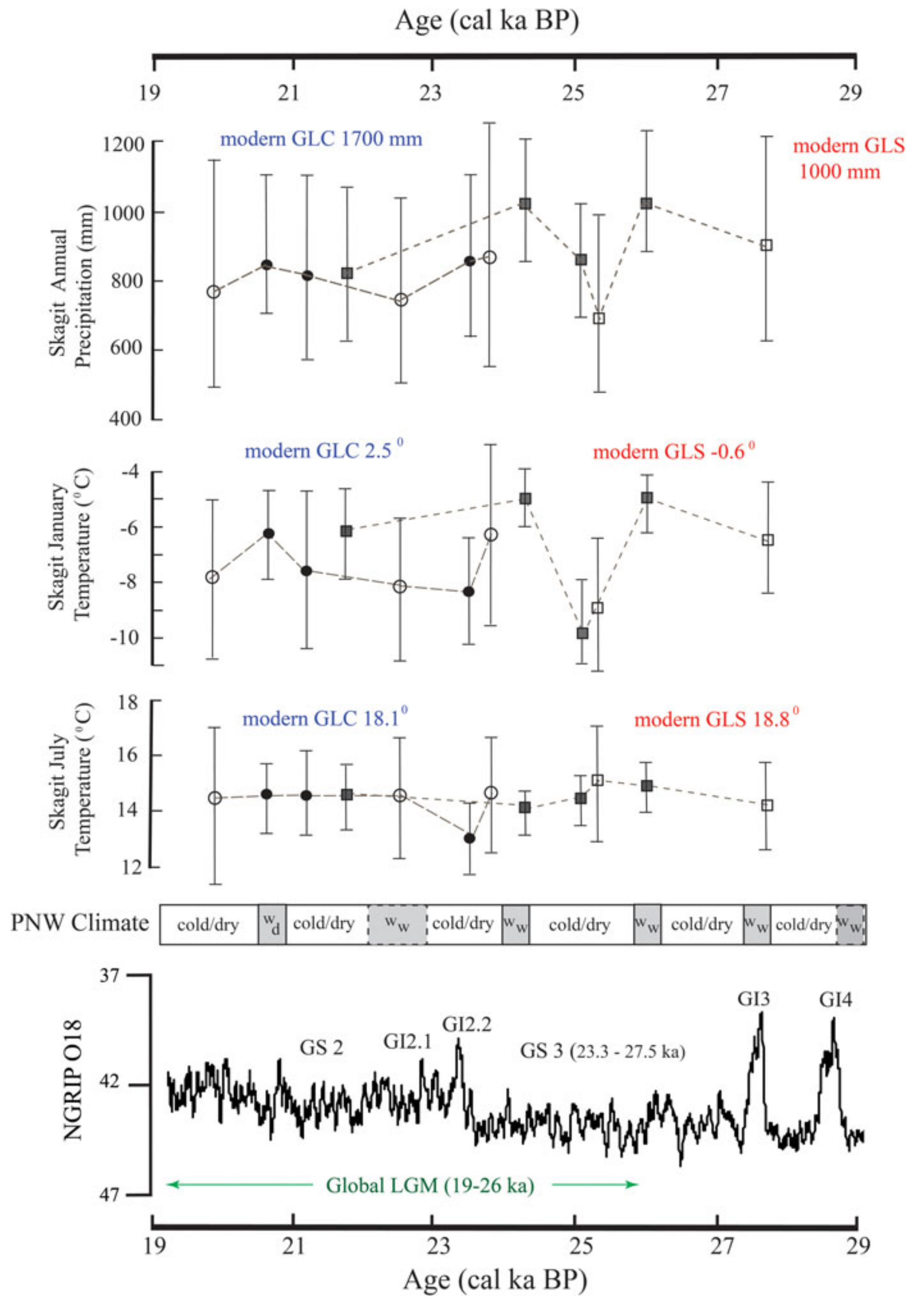

Figure 7. Last glacial maximum climate in Skagit Valley based on probability density function results for 14 indicator species at glacial Lakes Skymo (GLS; squares) and Concrete (GLC; circles; Table 1). Symbols are median values, and whiskers represent interquartile range in air temperature and annual precipitation estimates. Open symbols have large uncertainties due to a sample size of three or fewer (Table 3). Pacific Northwest (PNW) climate is a summary of Skagit Valley and other regional data. Gray boxes depict relatively warm/wet intervals. Dashed boxes are signals from other regional proxies not observed in the Skagit record. At bottom is the North Greenland Ice Core Project oxygen-isotope record of climate change based on GICC05 ages with Greenland climate stades (GS) and interstades (GI) (Svensson et al., 2008; INTIMATE Project Members, 2014).

Heusser and Igarashi (1994) noted that its range expanded well inland during the LGM, and its presence at GLC shows that it was at least 350 km south and 150 km inland of the nearest modern population (Heusser and Peteet, 1988). It has also been found in Port Moody interstadial sediments in the Fraser Lowland (Lian et al., 2001; Fig. 1) and in Late Pleistocene lake and bog cores on the western Olympic Peninsula (Heusser and Igarashi, 1994).

Dwarf birch and black crowberry heath are boreal-arctic species, and their presence in the GLS assemblages indicates that forest was discontinuous (Birks and Birks, 2014). Both tolerate extreme winter cold but are intolerant of warm summers. Dwarf birch is found today mainly north of 60° latitude at wet sites but, like northern spikemoss, extends south in alpine zones along the Rocky Mountains into British Columbia and Alberta (Thompson et al., 2015). The presence of abundant sedge achenes in most assemblages supports the conclusion that an open subalpine biome existed at lower elevations in Skagit Valley during the LGM.

Fluctuations in precipitation and temperature over the life of the glacial lakes led to repeated introductions of species adapted to different climates. Indicator species in the Skagit assemblages

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include those that favor drier (whitebark pine) or wetter (mountain hemlock) subalpine conditions, an open boreal/alpine climate (northern spikemoss, dwarf birch, heath), or a warmer temperate forest climate (Douglas-fir/western hemlock, grand fir, Sitka spruce) (Fig. 6).

The presence of mountain hemlock macrofossils in the 25.9 and 24.4 cal ka BP assemblages at GLS suggests that climate was relatively wet at these times (Fig. 7). Mountain hemlock is sensitive to drought (Minore, 1979) and requires an insulating snow cover that persists for at least 3 months to prevent its roots from freezing (Krajina, 1970; Wardle, 1974; Franklin and Dyrness, 1988). Increases in mountain hemlock pollen and macrofossils have been used as indicators of a shift to a wetter climate in this region in previous studies (Barnosky, 1984; Mathewes, 1993; Lian et al., 2001; Grigg and Whitlock, 2002; Herring et al., 2017).

Macrofossils of temperate forest species occur throughout the Skagit record but are not abundant (Fig. 6). The possible presence of Sitka spruce macrofossils in the Skagit assemblages 100 km inland from the Late Pleistocene Pacific coast is interesting. Sitka spruce can interbreed with Engelmann spruce where their ranges overlap (Farrar, 1995), and there is some difficulty in distinguishing needles of the two species (Supplementary Material 1). It is not tolerant of shade, has a moderate tolerance to frost, and prefers a hyper-maritime climate and nitrogen-rich soils (Franklin and Dyrness, 1988; Peterson et al., 1997). Its presence in upper Skagit Valley during the LGM may not be unusual because of the valley's low elevation and favorable microclimate along lakeshores. Sitka spruce is found today in lower Skagit and adjacent Fraser valleys (Krajina et al., 1982; Fig. 1). It occurs up to 1500 m asl in southwest British Columbia, and in the north its range expands inland 200 km along major river corridors (Sudworth, 1967; Peterson et al., 1997). In drier and colder climates, it occupies sites with high available soil moisture, such as floodplains and lake shorelines (Peterson et al., 1997). Considering these habitat requirements, Sitka spruce and northern spikemoss likely took advantage of the stable lake shoreline microclimates with moderated temperatures and higher soil moisture availability.

A few needles of noble fir (*Abies procera*) were found in the 25.9 and 24.4 cal ka BP warm assemblages at GLS (Fig. 6). This species is currently not found in the Skagit watershed but appears to have enjoyed a wider distribution during the LGM. Noble fir was likely extirpated from Skagit Valley during the ice sheet phase of glaciation that followed the LGM after 19 cal ka BP (Riedel, 2017).

Port Moody interstadial sediments in western Fraser Lowland include many of the same species as the Skagit Valley sediments, including Engelmann spruce, subalpine fir, bark and rove beetles, moss and leaf litter beetles, ground beetles, and weevils. Miller et al. (1985) interpreted the Port Moody assemblage to be an open forest community near the tree line. At times during the LGM, the continental climate and subalpine/alpine biome extended across much of the Puget and Fraser Lowlands (Hansen and Easterbrook, 1974; Barnosky, 1981, 1984; Hicock et al., 1982; Miller et al., 1985; Barnosky et al., 1987; Mathewes, 1991; Lian et al., 2001; Grigg and Whitlock, 2002; Ashworth and Nelson, 2014). The Skagit macrofossil assemblages confirm that this biome extended 100 km inland along unglaciated parts of the Skagit Valley floor during much of the LGM. Our data suggest that this biome likely extended into other mountain valleys not occupied by glaciers in the Cascade and southern Coast Mountains (Lian et al. 2001; Telka et al., 2003).

The Skagit macrofossil record and climate reconstructions have important differences from those on Olympic Peninsula (Fig. 1). In general, the Olympic coastal pollen, beetle, and macrofossil records depict a wet subalpine (parkland) forest biome (Heusser, 1972, 1983; Ashworth et al., 2021). In contrast, the Skagit LGM record, with abundant arid tree line species (whitebark pine and Engelmann spruce), indicates a drier subalpine biome like that in the Fraser and Puget–Willamette Lowlands.

LGM climate

The PDF results identified four broad patterns of climate change in the North Cascades during the LGM: (1) large decreases in precipitation and air temperature that were more pronounced in the west than the east (Figs. 5 and 7; Table 3); (2) a reduction of the steep climate gradient observed today; (3) a colder and drier trend from 25.9 to 21.7 cal ka BP (Fig. 7); and (4) millennial-scale variability in MAP and January air temperature (Fig. 7).

Our PDF estimates of air temperature during the LGM are comparable to regional pollen-based estimates. Our estimates of the change in median July temperature from today are 6.3 ± 1.5°C at GLS and 4.2 ± 2.1°C at GLC. Heusser (1972) estimated that mean July temperature was 5°C to 6.5°C cooler than at present on the Olympic coast. Whitlock (1992) suggested that mean annual temperature was 5°C to 7°C lower than at present at Battleground Lake in southern Washington between approximately 23.7 and 19.8 cal ka BP. Similarly, Barnosky (1981) inferred a reduction in mean annual temperature of 7°C during the same period at Davis Lake in southern Puget Lowland. Bartlein et al. (2011) estimated that mean annual air temperature in this region at 21 cal ka BP was more than 8°C lower than today. Global mean cooling at this time was 3°C to 5°C, with a Pacific Northwest air temperature 4°C to 8°C lower than today (Annan and Hargreaves, 2013). Our PDF estimate of the median value of annual temperature change (average of July and January estimates in Table 3) is about 7°C at GLC and 6°C at GLS.

January air temperature changed more than July air temperature at GLC, whereas the change between January and July temperatures at GLS was of the same magnitude (Fig. 7; Table 3). Bartlein et al. (2011) found that Late Pleistocene changes in winter temperature in North America were greater than summer temperature changes, a conclusion supported by Ashworth et al. (2021) on the Olympic Peninsula. We infer that a reduced marine influence on climate in western Skagit Valley during the LGM led to the relatively large 10°C change in winter air temperature at GLC. Air temperature changes were less pronounced at GLS, where the climate is more continental due to its location 75 km farther inland from the waters of Puget Sound.

Paleoclimate studies west and south of Skagit Valley have shown that MAP during the LGM was lower than today (Heusser, 1977; Barnosky, 1985; Grigg and Whitlock, 2002; Marshall et al., 2004; Bartlein et al., 2011). A summary of regional pollen data by Bartlein et al. (2011) led to an estimate of MAP 250–500 mm lower than today at 21.0 cal ka BP. Our estimates confirm regional aridity, with an average of 835 mm lower MAP at GLC and 100 mm lower at GLS (Fig. 7; Table 3). These results generally agree with Paleoclimate Modelling Intercomparison Project 3 data that predict a decrease of 700 mm/yr in the Pacific Northwest during the LGM (Braconnot et al., 2012).

The results of our study indicate that the strong modern precipitation gradient observed today within Skagit Valley did not exist during the LGM. The greater reduction in precipitation at

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GLC (50%) compared with GLS (10%) means that climate was essentially the same at the two sites. The Skagit record stands in contrast to that on Olympic Peninsula, where climate gradients steepened during the LGM (Porter, 1964; Ashworth et al. 2021).

Skagit Valley and the surrounding region were more arid during the LGM than today for at least two reasons. First, Pacific Ocean sea-surface temperatures were 4°C colder than today (Annan and Hargreaves, 2013), significantly reducing evaporation. Second, a more arid climate resulted from growth of continental ice sheets in Canada and their influence on atmospheric circulation (Braconnot et al., 2012). Development of the Laurentide high pressure system over the ice sheet accelerated and steered the jet stream and storms to the south (Oster et al., 2015). This led to a rise in pluvial lake levels in California and Nevada (Benson et al., 2003) and decreased precipitation in the Pacific Northwest (Barnosky et al., 1987; Thompson et al., 1993; Hostetler and Clark, 1997; Bartlein et al. 1998; Lian et al., 2001; Thackray, 2001; Grigg and Whitlock, 2002; Jiménez-Moreno et al., 2010; Oster et al., 2015).

Millennial-scale climate fluctuations

The PDF results reveal positive anomalies in the median values of three climate indices over the 8000-yr period of the record (Fig. 7; Table 3), due in part to the presence of temperate forest species (Figs. 5 and 6). Identification of significant changes is limited by the high variability in the PDF results resulting from the low number of species in some assemblages, and most changes are within the interquartile ranges of one another. Climate variability is expressed mainly as changes in January air temperature and MAP (Fig. 7). Although these changes seem to be more pronounced before 23 cal ka BP, the number of species used in the latter part of the reconstruction is relatively low (Fig. 7). Regional pollen studies, northeast Pacific Ocean sediment cores, and glacial geology have confirmed the existence of millennial-scale climate variability in this region during the LGM (Behl and Kennet, 1996; Pisias et al., 2001; Thackray, 2001; Grigg and Whitlock, 2002; Jiménez-Moreno et al., 2010; Riedel et al., 2010; Taylor et al., 2015).

The PDF results indicate that winters were warmer and climate overall wetter at 27.7, 25.9, and 24.4 cal ka BP at GLS, and from 21.2 until at least 20.7 cal ka BP at GLC. The magnitude of the changes are ±200 mm in MAP and ±2°C to +4°C in January air temperature (Fig. 7). The results for the 25.9, 24.4, and 21.2–20.7 cal ka BP assemblages are robust, because they contain a relatively high number of species for the PDF analysis and they have high assemblage diversity, with 24, 25, and 30–39 species, respectively (Table 2).

The PDF-based climate estimate for the 27.7 cal ka BP GLS assemblage is based on only three species, including needles of western hemlock/Douglas-fir and mountain hemlock (Fig. 6). Sediment cores from the Santa Barbara Basin provide evidence for a warm period at this time, based on increased bioturbation (Hendy and Kennet, 2000). Hebda et al. (2016) documented a decline in nonarboreal pollen and spikes in arboreal pollen, including mountain hemlock and pine, at Lynn Valley in southwestern British Columbia at about the same time as our 27.7 cal ka BP assemblage. Grigg et al. (2001) showed that western hemlock pollen increased at Little Lake, Oregon, at about the same time, and Marshall et al. (2017) documented peaks in Sitka spruce and subalpine fir needles at ca. 28 cal ka BP at the same site.

There is also regional evidence of warmer climate in the Pacific Northwest at approximately 25.9 cal ka BP, although limited age control precludes further correlations. Marshall et al. (2017) identified a peak in silver/grand fir, Sitka spruce, and mountain hemlock macrofossils at 25.4 cal ka BP at Little Lake in west-central Oregon; and Grigg et al. (2001) documented a peak in western hemlock and pine pollen at 25.8 cal ka BP in Fargher Lake (Figs. 1 and 8).

Climate was colder at GLS between 25.9 and 24.4 cal ka BP (Fig. 7). The 25.1 cal ka BP assemblage includes several open boreal alpine species, including the two boreal rove beetles discussed earlier, dwarf birch, black crowberry heath, and sedge. Sites from the Fraser Lowland to the western Olympic Peninsula and southern Washington show a change toward colder and drier conditions at about 25.0 cal ka BP, although the limiting ages have large errors (Fig. 8).

A relatively warm wet period at 24.4 cal ka BP is expressed by a diverse assemblage at GLS that includes temperate forest species (Figs. 6 and 7). Marshall et al. (2017) identified a minor peak in temperate forest macrofossils at 24 cal ka BP at Little Lake (Fig. 1). The K5 warm event at Kalaloch occurred at 24.5 cal ka BP (Ashworth et al. 2021), and a minor peak in mountain hemlock pollen was recorded at Bogachiel Bog at 24.2 cal ka BP (Heusser, 1978).

Climate became colder and drier again at GLS sometime after 24.4 cal ka BP, and by 23.5 cal ka BP, a cold climate is evident at GLC, with the lowest January and July temperature in our reconstruction (Table 3; Fig. 7). Temperatures likely declined during this part of the LGM with the decrease in summer insolation at this latitude and the growth of the ice sheets in the Northern Hemisphere (Berger, 1978).

The Skagit record has a gap between 23.5 and 22.7 cal ka BP. Grigg and Whitlock (2002) identified small increases in mountain hemlock and pine pollen at Fargher Lake between about 23.0 and 21.5 cal ka BP (Fig. 1). The 22.7 cal ka BP assemblage at GLC contains no temperate forest macrofossils and is dominated by 462 northern spikemoss megaspores and sedge achenes that are robust indicators of open boreal conditions. The 21.8 cal ka BP assemblage at GLS consists mainly of subalpine tree macrofossils. Nonarboreal taxa dominate pollen assemblages on western Olympic Peninsula (Heusser, 1974) and in southern Puget Lowland at this time (Barnosky, 1981; Barnosky et al., 1987; Fig. 8). At the K2 site near Kalaloch, Ashworth et al. (2021) recovered an insect assemblage indicative of cooling at 21.7 cal ka BP. Thackray (2001) suggested that this interval was the coldest part of MIS 2 (ca. 30–11.6 ka). Syntheses of global sea-surface temperature data have placed a narrower limit on the LGM at 22.3–19.0 cal ka BP (MARGO Project Members, 2009).

The 21.2 and 20.7 cal ka BP assemblages in lower Skagit valley are the most diverse in the record (Fig. 6; Supplementary Material 2 and 3). These assemblages include temperate forest species western hemlock/Douglas-fir, grand/silver fir, and possibly Sitka spruce that indicate climate warming (Fig. 6).

The two limiting ages for the Port Moody interstade in Fraser Lowland have a combined 2σ age range of 22.4–21.3 cal ka BP (our calibration; Hicock et al., 1982, 1999; Hicock and Lian, 1995; Fig. 8). We tentatively correlate this event to the taxonomically diverse 21.2 and 20.7 cal ka BP GLC assemblages, as the 2σ range for the older Skagit assemblage is 21.5–20.9 cal ka BP (Fig. 8; Supplementary Material 5).

Large errors in the ages of pollen zone boundaries in other studies limit correlation with the noncontinuous Skagit record

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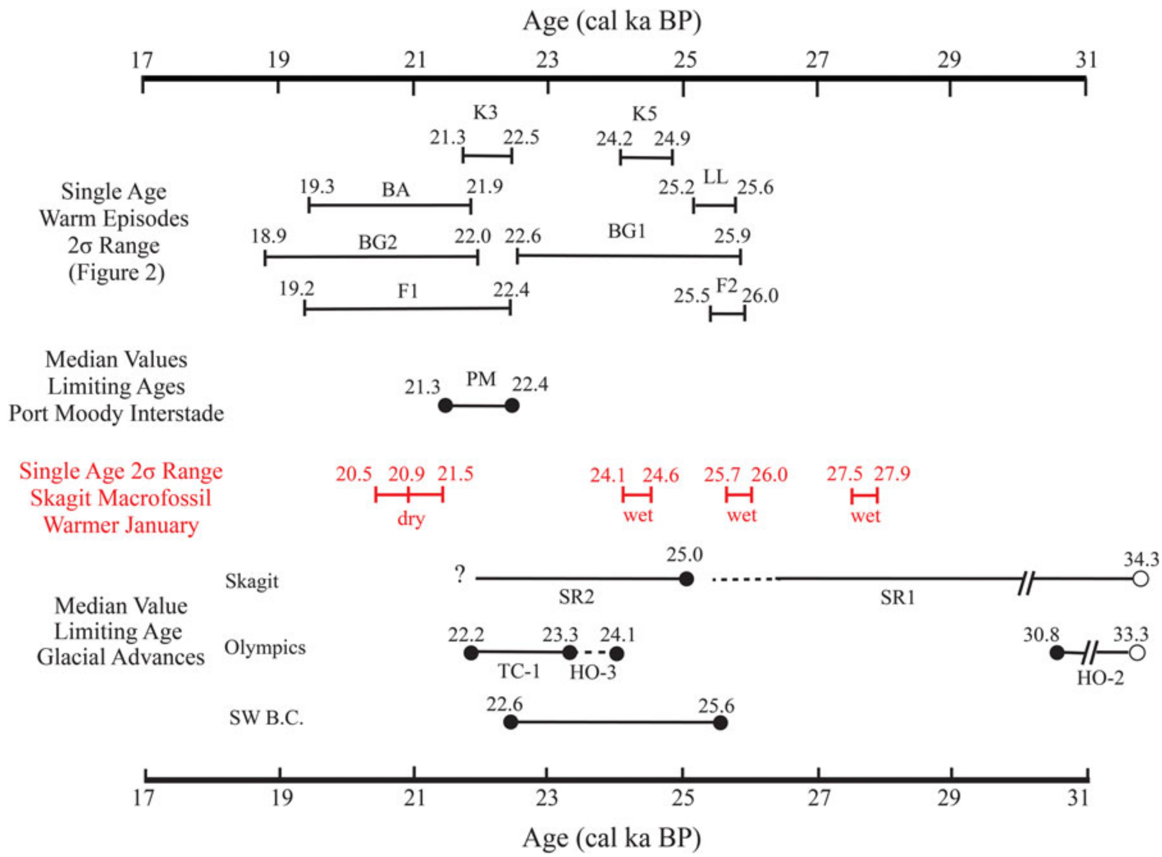

Figure 8. Comparison of calibrated radiocarbon ages for key glacial and biological events during the last glacial maximum, including pollen boundaries (same data sources as for Fig. 2) and alpine glacial advances: Hoh Oxbow 3 and Twin Creek 1 (Thackray, 2001), Skagit River 1 and 2 (Riedel et al., 2010), and Coquitlam (Hicock and Armstrong, 1981). All ages have been calibrated with the OxCal online program (Bronk Ramsay, 2009).

near the end of the LGM (Figs. 2 and 8). Four other sites in the Pacific Northwest record an increase in tree pollen and an associated decrease in nonarboreal pollen at about 20.7 cal ka BP (Figs. 1 and 2). They include Fargher Lake at 20.7 cal ka BP (Heusser and Heusser, 1980) and at Bogachiel Bog at about 20.4 cal ka BP (Heusser, 1978; Figs. 2 and 8). Western hemlock pollen increased after about 21.8 cal ka BP at Kalaloch (Heusser, 1977). Barnosky (1985) inferred an interstadial warm period between approximately 20.9 and 18.9 cal ka BP at Battleground Lake, and there is evidence of warming at this time at Carp and Little lakes (Grigg and Whitlock, 2002; Figs. 2 and 8).

Macrofossils are scarce in GLC assemblage at 19.8 cal ka BP. The age of this bed is derived from a single Engelmann spruce cone recovered below advance outwash from the ice sheet (Fig. 4). The ice sheet advanced from Puget Lowland into lower Skagit Valley sometime after 19.4 cal ka BP and reached its maximum extent at about 16.3 cal ka BP (Porter and Swanson, 1998; Troost, 2016; Riedel, 2017; Fig. 1).

Correlation with the alpine glacial record

The Skagit macrofossil and regional paleoenvironmental records are generally in accord with the fragmentary alpine glacial record in the Pacific Northwest. Our PDF analysis indicates that there were two relatively cold intervals, the first at ca. 25.1 cal ka BP (GLS) and a second at 23.5–21.2 cal ka BP (GLC) (Figs. 7 and 8). The times of these cold periods broadly correspond with alpine glacier advances in the region (Fig. 8; Supplementary Material 5). Skagit Valley alpine glaciers advanced at least twice during the LGM, first between 34.3 and 25 ka, and later sometime after 25 ka, at which time they achieved their maximum late glacial extent (Riedel et al., 2010). Our results provide a refinement of that chronology, as they indicate that the earlier advance may have ended before 25.9 ka, and the later advance may have begun after the 24.4 cal ka BP warm-wet period. The Coquitlam advance in south-coastal British Columbia occurred after about 25.6 cal ka BP (Hicock and Armstrong, 1981; Riedel et al., 2010; Fig. 8). The Hoh Oxbow 3 glacier advance on western Olympic Peninsula occurred after 24.1 ka, and the Twin Creek 1 advance in the same area has been dated to about 23.3–22.2 ka (Thackray, 2001).

Clark and Bartlein (1995), Hicock et al. (1999), and Thackray (2001) concluded that millennial-scale climate oscillations controlled the advance and retreat of glaciers, respectively, in the western United States, Fraser Lowland, and on western Olympic Peninsula. Hostetler and Clark (1997) concluded that changes in air temperature were primarily responsible for the advance and retreat of alpine glaciers in the Yellowstone area and in Idaho. Thackray (2008) suggested that glaciers farther west were influenced more by precipitation than temperature. Our PDF results indicate that MAP fluctuated by ±200 mm early in the Skagit record (Fig. 7). These changes may have controlled the mass balance of Skagit alpine glaciers, because the climate was relatively arid and summer air temperatures changed little (Fig. 7). Modern mass balance data suggest that alpine glaciers on the more arid eastern flank of the North Cascades are more sensitive

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to changes in precipitation than temperature (Riedel and Larrabee, 2016). The lack of a more accurate glacial chronology hinders further comparisons.

Correlation with the Greenland ice core record

Regional alpine glacial advances in the Pacific Northwest and changes in sea-surface temperatures and pollen have been compared with the North Atlantic record of climate (Clark and Bartlein, 1995; Hicock et al., 1999; Hendy and Kennett, 2000; Pisias et al., 2001; Grigg and Whitlock, 2002; Jiménez-Moreno et al., 2010). Changes in oxygen isotope composition in Greenland ice cores provide a continuous, high-resolution record of millennial-scale oscillations in climate in the North Atlantic, known as Dansgaard–Oeschger (D-O) cycles (Dansgaard et al., 1993). D-O cycles, which occurred about every 1400 yr during the last glacial cycle, are marked by abrupt initial warming (interstade) and subsequent long slow cooling (Fig. 7). Jiménez-Moreno et al. (2010) suggested that the Greenland interstades (GI) were marked by a warm-wet climate in North America, while stades (GS) were cold and dry. Another feature of the LGM climate in the North Atlantic is Heinrich events, which are associated with increases in the discharge of icebergs and cold water from the Laurentide ice sheet (Heinrich, 1988; Bond et al., 1993).

Warm-wet winters in the Skagit macrofossil record and alpine glacier activity generally correlate with millennial-scale climate variability in the North Atlantic (Fig. 7). Greenland interstade GI3 occurred at about the same time as the Skagit 27.7 cal ka BP warm-wet period (Svensson et al., 2008; INTIMATE Project Members, 2014; Fig. 7). Regional alpine glacial advances in the Pacific Northwest broadly coincide with stades GS3 and GS2 (Hicock et al., 1999; Thackray, 2001; Riedel et al., 2010). The only Heinrich event that occurred during the period of the Skagit macrofossil record is H2 (26.5–24.3 cal ka BP). This event coincides with the end of GS3 (27.5–23.3 cal ka BP; Fig. 7). Warm-wet periods at 25.9 and 24.4 cal ka BP in the Skagit record were separated by a cold period that may correspond to H2. The late LGM warm period in the Pacific Northwest, observed in the Skagit record at 21.2–20.7 cal ka BP, occurred during GS2 (Figs. 7 and 8). Although not correlated with named interstades in the ice core record, all three of the later warm-wet winter Skagit events generally coincide with smaller peaks in the North Greenland Ice Core Project record (Fig 7).

The gap in the Skagit record from 23.5 to 22.7 cal ka BP spans Greenland interstades GI2.1 (23.2 cal ka BP) and GI2.2 (23.0 cal ka BP) (INTIMATE Project Members, 2014; Fig. 7). Other regional paleoenvironmental warm periods may correlate with these interstades. Grigg and Whitlock (2002) identified increases in mountain hemlock pollen at 23.0 cal ka BP, followed by an increase in arboreal pollen until 21.0 cal ka BP at Fargher Lake. Hicock and Lian (1995) and Lian et al. (2001) reported median maximum limiting dates of 22.9 and 22.4 cal ka BP for the beginning of the Port Moody interstade in the lower Fraser Valley (Figs. 2 and 8). The overlap in many of the dates from this region precludes more definitive correlation of these late LGM events with GI2.1 and GI2.2.

Causes of millennial-scale climate changes

A long, gradual cooling and drying trend during the LGM is evident in the Skagit macrofossil record (Fig. 7). Superimposed on this orbital-scale change are millennial-scale changes in climate in Skagit Valley expressed as increases in winter air temperature (+2°C to +4°C) and MAP (+200 mm). Millennial-scale climate variability occurred across western North America and is thought to be related to changes in the Atlantic Meridional Overturning Circulation and its influence on global heat transfer (Harrison and Sanchez Goni, 2010). In the northeast Pacific region, the fast response of marine and terrestrial proxies to D-O events indicates that changes in atmospheric circulation may have been responsible for transmission of millennial-scale variability from the North Atlantic (Hendy and Kennet, 2000; Taylor et al. 2015). Recent model simulations indicate that the locations and strengths of the Aleutian Low, the Laurentide ice sheet High, and the North Pacific High controlled the latitude of the westerly jet stream and delivery of moisture to western North America during the LGM (Oster et al., 2015). One potential mechanism for transmission of millennial-scale changes in climate from the North Atlantic to the North Pacific may have been the Intertropical Convergence Zone (ITCZ) and its influence on advection of warm tropical water north via the California Underwater Current, the location of the westerly jet stream, and the strength and position of semipermanent pressure systems in the northeast Pacific (Zhang and Delworth, 2005; Leduc et al., 2009; Deplazes et al., 2013; Okumura et al., 2009; Taylor et al., 2015; Oster et al., 2015). During cold D-O phases in the North Atlantic, the ITCZ and westerly jet stream shifted south, leaving the northeast Pacific drier. Warm D-O events shifted the ITCZ and the jet stream northward, producing wetter conditions in the Pacific Northwest, including Skagit Valley.

CONCLUSIONS

Skagit Valley macrofossil assemblages provide a rare glimpse into the climate and ecology in the North Cascade Range at the LGM. Large parts of the valley floor were refugia for 8000 yr before invasion by the Cordilleran ice sheet. Macrofossil-bearing glacial lake beds survived subsequent ice sheet glaciation in gullies protected by valley bedrock spurs and beneath thick interlobate deposits.

The Skagit refugia were an extension of an arid boreal (subalpine) forest biome that at times included temperate forest and alpine tundra species. This biome extended from southern Puget Lowland northward to the western Fraser Lowland and as far as 150 km into unglaciated parts of Skagit Valley. Like many ice age communities, those in Skagit Valley included a mix of species found today at a wide range of elevations and latitudes. The GLC refugium hosted a more diverse community than the GLS refugium, likely because it was 400 m lower in elevation.

The PDF method is an effective tool for quantifying climate change based on the presence of macrofossils. Our PDF results are consistent with previous estimates of climate change in this region at the LGM, even though our analysis was limited by a small number of species in 5 of the 12 assemblages.

Our results indicate a 10% to 50% decrease in MAP during the LGM. January air temperatures changed more than summer temperatures at both glacial lakes, with a 6°C to 10°C reduction in January temperatures and a 4°C to 6°C decrease in July temperatures (Fig. 7). Winter temperature and MAP changes are larger at GLC, where the modern climate is maritime, whereas summer temperature change is larger at GLS, where the modern climate is continental.

The larger decreases in MAP and air temperature in lower Skagit Valley compared with the upper valley meant that the strong climate gradient observed today between the two sites

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was eliminated during the LGM. This contrasts with the steepened climate gradients during the LGM on Olympic Peninsula.

Ten calibrated radiocarbon ages on the Skagit Valley macrofossil assemblages provide a chronology for the terrestrial responses to millennial-scale changes in climate in this region. These changes are expressed as increases in January air temperature (+2°C to +4°C) and MAP (+200 mm) in individual assemblages dated at 27.7, 25.9, 24.4, and 21.2–20.7 cal ka BP.

Future work on the Skagit sections may include pollen analysis and detailed examination of other taxa, such as chironomids and coleopterans, which have already been extracted from the lake beds. The macrofossils from the Skagit Valley assemblages are also a potential source of genetic material for phylogeography studies.

Supplementary Material. The supplementary material for this article can be found at https://doi.org/10.1017/qua.2021.50.

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