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Climate and vegetation since the Last Interglacial (MIS 5e) in a putative glacial refugium, northern Idaho, USA

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A B S T R A C T

There are very few terrestrial sediment records from North America that contain a nearly continuous sequence spanning from the Last Interglacial period to the present. We present stratigraphic records of pollen and several other proxies from a *Carex*-dominated wetland, Star Meadows, located 140 km south of the maximum extent of the Cordilleran Ice Sheet and near the current southern extent of interior mesic forests in northern Idaho. Many species in this region are disjunct by 160 km of arid steppe and dry forest from their more extensive distribution along the Pacific Northwest coast and may have survived in an interior refugium. The chronology for the upper 251 cm was determined by six radiocarbon dates and one tephra deposit, and the age of the remainder of the core (251–809 cm) was estimated by correlation with SPECMAP $\delta^{18}O$. Fluctuating water levels were inferred from alternating peat, biogenic silica, and aquatic pollen types. During MIS 5e the region was warmer and drier than today and was dominated by *Pinus* (likely *Pinus contorta*) mixed conifer forest surrounding a *Carex* meadow. A cool-moist climate (MIS 5b–5d) soon developed, and the site was inundated with deep water. Pollen indicated wetland vegetation (*Betula glandulosa*, Typhaceae, and *Salix*) developed around a lake with a *Pseudotsuga/Larix* and *Picea* forest on the surrounding slopes. During MIS 5a, a warmer climate supported a *Pseudotsuga/Larix*, *Abies*, and *Picea* forest on the surrounding hillsides and a *Carex*-dominated environment within a dry meadow. From MIS 4 to MIS 3, a cool and wet *Pinus* and *Picea* forest predominated. Water levels rose, enabling *Nuphar* to persist within a perennial lake while a sedge fen established along the lake margin. As climate transitioned into MIS 2, a cooler and drier climate supported a *Pinus* and *Picea* subalpine parkland, though water levels remained high enough to support *Nuphar*. During the Last Glacial Maximum the sediment was mainly silt and clay with high *Artemisia* and very poor pollen preservation. Glaciers descended to 500 m elevation above Star Meadows in adjacent drainages suggesting a periglacial environment occurred at the site. Lake level decreased through the Pleistocene–Holocene transition (ca. 11.7 ka) and the site returned to a sedge peatland surrounded by an open *Pinus* forest. The most striking vegetation change occurred in the middle to late Holocene with the first occurrence and then later dominance of Cupressaceae pollen, most likely *Thuja plicata*, which is a dominant species in modern interior mesic forests. The late Holocene vegetation was uniquely mesic in the context of the last 120,000 years, casting doubt on this region serving as a glacial refugium.

1. Introduction

In western North America there are very few terrestrial sediment core records that span the interval from the last major interglacial, marine isotope stage (MIS) 5e (ca. 130 to 123 ka, or thousands of calendar years before present), through the Last Glacial Maximum (LGM; 26–19 ka), to the present. For the region south of the Cordilleran Ice Sheet (i.e., Washington, Oregon, northern California, and Idaho) vegetation and climate records that span the last 130 ka have been obtained from only a few sediment cores (Heusser and Shackleton, 1979; Adam et al., 1981; Whitlock and Bartlein, 1997; Heusser et al., 1999; Whitlock et al., 2000; Herbert et al., 2001; Lyle et al., 2001; Pisias et al., 2001; Woolfenden, 2003; Jiménez-Moreno et al., 2007). Therefore, little is known about how major vegetation types in the region south of the Cordilleran Ice Sheet responded to changing climates during the Last Interglacial and subsequent stadial and

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interstadial events of the late Quaternary (Jiménez-Moreno et al., 2010). During the LGM considerably more evidence indicates reduced forest cover and increases in pollen types typical of cold and dry climates, in agreement with paleoclimate simulations (Grigg and Whitlock, 2002; Braconnot et al., 2007; Thompson, 2007). However, most of these records occur within the Coast and Cascade ranges of Oregon and Washington. Currently no paleovegetation records exist in the northern Rocky Mountains that spans the LGM (reviewed in Thompson, 2007), the closest such site being Carp Lake in Washington (Whitlock and Bartlein, 1997; Whitlock et al., 2000). In contrast, there are several records in the northern Rocky Mountains spanning the Lateglacial and Holocene periods (Mehringer et al., 1977; Karsian, 1995; Doerner and Carrara, 1999, 2001; Millspaugh et al., 2000; Brunelle and Whitlock, 2003; Millspaugh et al., 2004; Brunelle et al., 2005; Power et al., 2006).

A distinctive feature of the vegetation of the northern Rocky Mountains is a zone of mesic forests extending northward from northern Idaho. These mesic forests are unique because they support at least 22 endemic plant species and more than 100 vascular plant species (including the canopy-dominant tree *Thuja plicata*) that are disjunct from their main population distribution along the Pacific Northwest coast (Björk, 2010). It remains unclear whether most species in the inland disjunction survived the glacial periods within a north–Idaho refugium, or whether these species were recently dispersed from coastal populations (Gavin, 2009). In the past decade, several studies have taken a genetic approach to this question (Brunsfeld and Sullivan, 2005; Brunsfeld et al., 2007; Carstens and Richards, 2007). These phylogeography studies provide broad support for the presence of a glacial refugium for at least two plant and three amphibian taxa within the Clearwater Range of northern Idaho (Ritland et al., 2000; Nielson et al., 2001; Carstens et al., 2004; Brunsfeld and Sullivan, 2005; Thompson and Russell, 2005; Brunsfeld et al., 2007). However, few paleovegetation or paleoclimate records exist from the interior mesic forests, and none that extend to the LGM or earlier, to support these inferences of refugia.

In this study, we present a late Pleistocene and Holocene vegetation and climate record from a nearly continuous sediment and peat core located near the southern end of the distribution of the mesic *T. plicata* forests in northern Idaho (Fig. 1). The study site, Star Meadows, is adjacent to the Lochsa River, and 140 km south of the maximum extent of the Cordilleran Ice Sheet. Although the mountains in the surrounding area, especially to the north and at high elevations, underwent extensive glaciation during the Pleistocene, Star Meadows is located down-valley of late Pleistocene terminal moraines (Fig. 1b). The Lochsa River and other river canyons in the surrounding Clearwater National Forest comprise the putative glacial refugia (Daubenmire, 1975; Brunsfeld and Sullivan, 2005; Brunsfeld et al., 2007; Carstens and Richards, 2007). To reconstruct the environmental context of this region, we used a combination of fossil pollen and sediment composition (biogenic silica and measures of inorganic and organic matter) to infer the past climate and vegetation history of the interior mesic forests. If this region existed as a mesic refugium in the past, then the pollen record should reveal indicators of a mesic climate, such as continuous forest cover or the presence of mesic-adapted taxa, through the LGM.

2. Methods

2.1. Site description and field collection

Star Meadows is a 3.2 ha seasonally inundated meadow located on undulating terrain at 1109 m a.s.l. and 53 m above the Lochsa River in northern Idaho (Fig. 1). The elevation of the outlet at the northern end of the meadow indicates that only 20 cm of water can fill the modern meadow. The meadow and other wetlands are located on the apparent run-out of a massive landslide from the south side of the Lochsa River (Fig. 1c). The wetland depressions may have originated from abandoned channels of the Lochsa River created before the river down-cut through the landslide debris. The vegetation of Star Meadows is dominated by *Carex aquatilis*, *Comarum palustre*, and other *Carex* spp. (Fig. 1d). *Sphagnum* is limited to the southwestern edge of the meadow. The surrounding forest is dominated by *T. plicata* along with *Abies grandis*, *Pinus monticola*, and *Picea engelmannii*. *Pseudotsuga menziesii* and *Larix occidentalis* are restricted to well-drained microsites; the warmest southern exposures may support occasional *Pinus ponderosa*. A survey of the forest understory revealed 148 vascular plant species (Curtis Björk, personal communication, 2013). Common vascular plant and fern species include *Adiantum pedatum*, *Asarum caudatum*, *Coptis occidentalis*, *Disporum hookeri*, *Fragaria virginiana*, *Galium triflorum*, *Goodyera oblongifolia*, *Gymnocarpium dryopteris*, *Linnaea borealis*, *Smilacina stellata*, *Tiarella trifoliata*, and *Viola orbiculata*. *T. plicata* occurs up to 1675 m in elevation and is most abundant on riparian or poorly-drained sites below 1400 m (Daubenmire, 1980; Cooper et al., 1991). Moving below 1000 m and towards warmer and drier sites, *A. grandis* and *P. menziesii* become increasingly important. Above 1400 m, *T. plicata* forests transition into subalpine forests that are dominated by *Abies lasiocarpa*, *Pinus contorta*, and/or *Tsuga mertensiana*. Tree line within the Bitterroot Mountains does not often extend higher than 2300 m.

Despite its interior location, the study region experiences a maritime west-coast climate with snowy winters. Weather-station data are available within 2.5 km of the site (http://www.wrcc.dri.edu). Mean annual precipitation is 97 cm with somewhat drier summers (15% annual precipitation occurs June–August) than winters (35% precipitation occurs December–February). Snow cover persists, on average, from mid-November to early April. In July the daily maximum and minimum temperatures are 27.6 °C and 7.2 °C, respectively (average = 17.3 °C). In December the daily maximum and minimum temperatures are −1.2 °C and −9.1 °C, respectively (average = −5.2 °C).

In August 2010 we obtained an 809 cm long core from the visually wettest location (46°30′56.8″N, 114°40′55.7″W) of the meadow using a modified square-rod Livingstone piston corer (Wright et al., 1984). To reduce friction from sediment along the drive rods, between each Livingstone core drive we widened the core hole with a bucket auger attached to drive rods. However, at 8 m depth the resistance became too great to continue coring. Continued use of the bucket auger, which could not retrieve samples, indicated peaty sediment continued to at least 9 m. During the recovery of two core sections, the piston slipped resulting in the loss of two short segments (342–367 cm and 698–706 cm). A second core (91.5 cm) was taken three meters from the first core, in order to ensure that we recovered a continuous sediment sequence above the Mazama ash, 7.63 ka. We extruded and wrapped each core section in the field. We transported the core to the University of Oregon and stored it at 4 °C.

2.2. Laboratory analysis

2.2.1. Core description, magnetic susceptibility, CT-Scan, organic content, and biogenic silica

We split the cores longitudinally and described the sediment stratigraphy by visual and microscopic inspection. Lithology was described following Schnurrenberger et al. (2003). The upper 91.5 cm of the cores were correlated by visual inspection. We

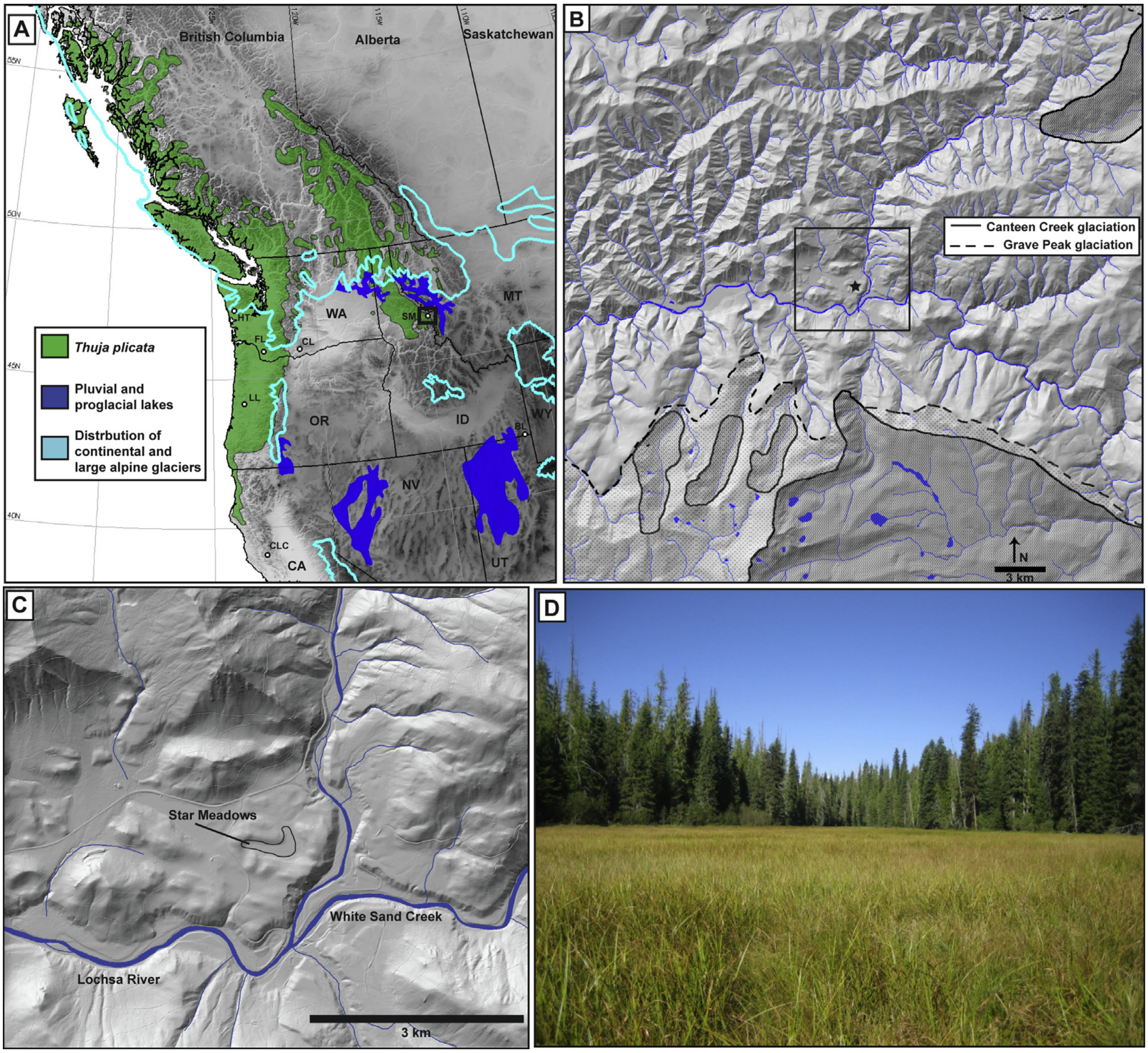

Fig. 1. (A) The modern distribution of *Thuja plicata* in north-west North America (Little, 1971) plotted on a shaded relief map. Also shown are the locations of major pluvial lakes, proglacial lakes, and ice extent at 17 ka (Dyke et al., 2003). The location of Humptulips (HT; Heusser et al., 1999), Fargher Lake (FL; Grigg and Whitlock, 2002), Carp Lake (CL; Whitlock and Bartlein, 1997; Whitlock et al., 2000), Little Lake (LL; Grigg et al., 2001), Clear Lake (CLC; Adam et al., 1981), Bear Lake (BL; Jiménez-Moreno et al., 2007), and Star Meadows (SM) are also noted. Square indicates enlarged map in (B). (B) Shaded relief map showing the location of Star Meadows (star icon) in the Lochsa River watershed. Late Pleistocene glacier extent corresponds to two glaciations mapped by Dingler and Breckenridge (1982). Square indicates enlarged map in (C). (C) Shaded relief LIDAR map showing the location of Star Meadows on a landslide run-out. (D) Photograph of Star Meadows showing the surrounding forest (dominated by *Thuja plicata*) and meadow vegetation (mainly *Carex* spp.).

measured magnetic susceptibility using a Bartington MS2 meter at one-cm intervals and photographed each core section using a line-scan camera on a GEOTEK "bench-top" split core MSCL-XY track (Marine Geology Repository at Oregon State University).

Bulk density was measured on 44 samples (1 cm^3), followed by measurement of organic content using loss-on-ignition (at 550 °C). To estimate bulk density at a resolution of ca. 0.5 mm, we scanned the core using a Toshiba CT-scan at Oregon State University College of Veterinary Medicine. We selected a longitudinal image of each core image using RadiAnt (free software; http://www.radiantviewer.com/) to locate the section with the fewest cracks, void spaces, and sediment disturbance due to root growth. Radio-opacity values were averaged at each depth along a 5-mm wide transect using ImageJ (free software; http://rsbweb.nih.gov/ij/). To express the opacity values as bulk density, we developed a linear relationship between measured bulk density ($n = 44$) and the corresponding opacity values ($r^2 = 0.897$).

We analyzed percent organic carbon and nitrogen on 155 subsamples every ca. 5 cm using a Costech ECS 4010 CHN analyzer at the University of Illinois at Urbana–Champaign. Samples were oven dried and ground with a mortar and pestle until the samples had the consistency of a fine powder prior to analysis.

A total of 205 samples were analyzed for biogenic silica (BSi) using a wet digestion extraction procedure outlined by Mortlock and Froelich (1989). After six hours of digestion in a hot sodium carbonate solution, we assayed for Si concentration using the molybdate-blue method (Mortlock and Froelich, 1989).

2.2.2. *Chronology*

Six accelerator mass spectrometry (AMS) radiocarbon dates were obtained from the sediment core. We attempted to find charcoal or wood for each radiocarbon date, but at four depths we resorted to dating a 1 cm^3 sample of bulk sediment (pre-treated with 10% KOH and 10% HCl). The sediment of these samples was highly decomposed peat and the resultant dates are concordant with tephra and other dates of macrofossils and thus consistent with an absence of a hard-water effect. Radiocarbon dates were calibrated to calendar years BP and rounded to the nearest decade using CALIB 5.0 (Stuiver and Reimer, 1993; Reimer et al., 2004). We created an age model using CLAM (Blaauw, 2010) with a monotonic spline between the six AMS dates and the Mazama tephra layer (Zdanowicz et al., 1999) for the portion of the core that was dateable by radiocarbon (<251 cm).

Absolute dating of the lower 558 cm of the core (older than 50,000 years) was not possible due to the absence of mineral matter suitable for optical-spin luminescence dating. To estimate the ages of this portion of the core, we noticed a strong visual correlation of percent organic carbon and the SPECMAP (Imbrie et al., 1984) $\delta^{18}O$ record, which would be expected if warm periods resulted in greater organic matter production. We attempted to use the NGRIP $\delta^{18}O$ record (North Greenland Ice Core Project Members, 2004), but the resolution of the Star Meadows core was not as high as the NGRIP record and the age of Star Meadows may exceed that of NGRIP. We created two age models with alternative tie points between SPECMAP (1000-year resolution) and Star Meadows to determine which match had the strongest correlation. We employed several rules in order to be consistent with each model: 1) all tie points between the percent organic carbon curve and $\delta^{18}O$ curve were limited to depths below the oldest radiocarbon age (251 cm), and 2) only two tie points, one at a peak and another at a trough in the organic carbon curve, were assigned to each pollen zone (see below for pollen zonation). In other words, for each peak (or trough) in percent organic matter, we selected a specific peak (or trough) in $\delta^{18}O$ from SPECMAP. We selected the age model that yielded the highest correlation and that also produced an overall climate reconstruction that was consistent with glacial-maximum and interglacial periods.

2.2.3. *Pollen analysis*

We processed 179 (0.5 cm^3) samples for pollen analysis following standard methods (Krzywinski et al., 2000) with the addition of a second KOH extraction. Processed samples were stained and pollen was examined at 400× magnification. We identified pollen to the lowest taxonomic level possible based on published keys (Kapp, 2000; Krzywinski et al., 2000) and the modern pollen reference collection at the University of Oregon. Asteraceae pollen types were differentiated into four categories: Tubuliflorae-type (sunflower); *Ambrosia*-type (bursage); Liguliflorae-type (lettuce subfamily), and *Artemisia* (sagebrush). *Pinus* (pine) grains were differentiated into *Pinus* and *Strobus* subgenera-types based upon the presence or absence of verrucae on the leptoma. All aquatic pollen types, algae, and Cyperaceae were excluded from the pollen sum. Cyperaceae was excluded from the total pollen sum because the meadow is currently dominated by *Carex* spp. We identified a minimum of 350 terrestrial pollen grains in the pollen sum, resulting in 367–953 total identified pollen grains per sample.

After all samples were counted, 10 *Betula* grains were measured at 20 levels in order to differentiate *Betula* grains to species level (*Betula glandulosa* or *Betula papyrifera*). *Betula* grain pore size and diameter were measured following the procedures outlined by Ives (1977) and Clegg et al. (2005). Pollen zones are based on a constrained cluster analysis (Grimm, 1987) using the total sum of squares method. Placement of zone boundaries also was guided by other sediment properties (i.e., percent organic carbon and biogenic silica).

3. Results

3.1. *Core description, magnetic susceptibility, CT-Scan, organic content, and biogenic silica*

The lithology of the Star Meadows core alternates between highly fragmental granular peat, sapropel, and sapropelic clays (inorganic silt and clay; Schnurrenberger et al., 2003; Fig. 2). We used the term fragmental granular peat to describe each of the peat layers because they consisted of fragments of herbaceous and woody plant parts between 0.1 mm and 2 mm in size. Below 510 cm the sapropel and peat units are marked by several very thin (<1 cm) beds that consist of slight color changes (black and dark brown). Contacts between adjacent units are generally diffuse spanning 2–3 cm, except for a sharp transition above a unit of light brown silt and clay (314–298 cm) and at the start of the Mazama tephra (90–73 cm). Also notable was slight orange and green mottling in a low-organic silt and clay unit from 124 to 90 cm. High-resolution line-scan photographs are in the Supplementary material.

Percent organic carbon varies from 0.3 to 59.7%. The highest percent organic carbon occurs within the peat-rich sediments (0–20, 514–549, and 734–809 cm). The lowest percent organic carbon occurs in clay and tephra-rich sections (64–175 cm) (Fig. 2). Percent organic nitrogen varies from 0.03 to 3%. Variations in percent organic nitrogen mirror fluctuations in percent organic carbon, with the highest percentages occurring in the fragmented granular peat sections. C:N ratios, with the exception of five samples, are greater than 10 indicating the source of sediment was mainly terrestrial (Meyers, 1994). The C:N ratio is greater in the lower two peat segments (21–34 and 18–45 respectively), suggesting almost no aquatic organic matter sources. The percent of biogenic silica (BSi) varies from 0.6% (784 cm) to 54.9% (40 cm). The highest percentages (>40%) of BSi occur near the top (30–67 cm). There are three sections (103–137, 514–559, and 757–802 cm) containing <6% BSi.

Bulk density estimated from radio-opacity (CT-scan) varied between 0.1 and 1.2 g/cm^3. A total of four peaks in bulk density were observed occurring at 79, 106, 212, and 297 cm. Magnetic susceptibility (MS) varies from -1.3×10^{-5} to 2.5×10^{-5} SI with major peaks at approximately the same depths as high bulk density values. The lowest MS values occur at depths with high organic content.

3.2. *Chronology*

For the top 251 cm of the sediment core, a constrained spline age–depth model was fit to six AMS radiocarbon dates (all in stratigraphic order) and one tephra to create a chronology (Table 1; Fig. 3). For the remainder of the core, we examined correlations between alternative age assignments for the percent organic carbon and the $\delta^{18}O$ record from SPECMAP. The first age–assignment model placed the base of the core at ca. 227 ka ($r = -0.66$) (Fig. 3). The second model estimated the base at ca. 125 ka ($r = -0.61$). Additional attempts could not yield a higher correlation. We used the climatic interpretation of the pollen and sediment proxies to choose between the two models. We found no clear evidence of the penultimate (Illinoian) glaciation (MIS 6) in the sediment or pollen records that is similar in organic content and pollen assemblages to the LGM. There was also no evidence of any tephra deposits (i.e. Medicine Lake andesite tuff, various tephras from Mt. St. Helens, and Summer Lake JJ) below 251 cm that could provide additional age constraints (Herrero-Bervera et al., 1994; Whitlock et al., 2000; Lanphere et al., 2002; Colman et al., 2006; Kuehn, personal communication, 2014). Therefore, we chose the younger age model (125 ka), which places the base of the core within MIS 5e. MIS

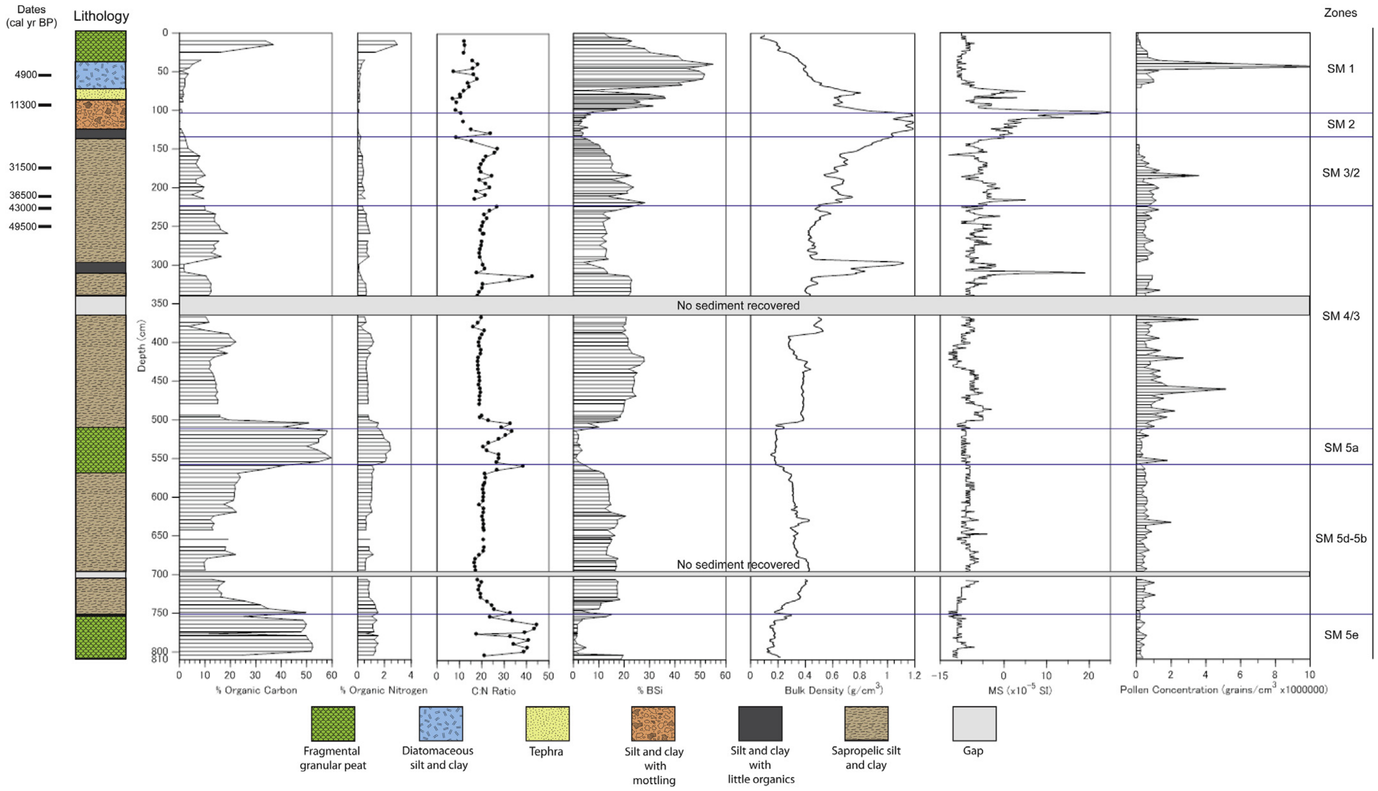

Fig. 2. Sediment composition (% organic carbon, % organic nitrogen, C:N ratio, % BSi, bulk density, magnetic susceptibility (MS), and pollen concentration) of the Star Meadows core.

Table 1
AMS radiocarbon dates from Star Meadows, Idaho. All samples were analyzed at the Center for Accelerator Mass Spectrometry (CAMS) at Lawrence Livermore National Laboratory. Calibrated dates were made with the INTCAL13 calibration curve (Reimer et al., 2004).

Depth (cm)	Laboratory number (CAMS)	^{14}C age (yr BP)	Calibrated age (median cal yr BP and 2 σ range)	Material dated
58–59	160861	4300 ± 220	4880 (4300–5500)	~60 pieces of charcoal
96–97	155160	9845 ± 40	11,240 (11,200–11,300)	1 cm^3 bulk sediment
177–178	155161	27,300 ± 130	31,450 (31,200–31,700)	1 cm^3 bulk sediment
213–214	155162	32,120 ± 380	36,500 (35,300–37,700)	1 cm^3 bulk sediment
230–231	151036	38,630 ± 430	42,950 (42,200–43,700)	1 cm^3 bulk sediment
250–251	156033	46,370 ± 560	49,450 (48,470–50,000)	Single piece of wood

stages were then assigned to each pollen zone based on sediment composition and vegetation assemblage interpretations (Figs. 3 and 4).

In order to avoid confusion between MIS ages and pollen zones, pollen zones were labeled as the MIS stages they were assigned. Zones SM 3/2 to SM 1 were within the range of radiocarbon dating and zone-boundary ages were rounded to 100 years. Zones SM 5e to SM 4/3 were outside the ^{14}C-dated period and correlation-assigned ages were estimated to within 1000 years using a visual correlation to the SPECMAP δ^{18}O record as described above.

3.3. Pollen

Pollen was generally well preserved, but concentrations were highly variable (9×10^3–1.1×10^7 grains/cm^3; Fig. 2). Pollen could not be recovered from sediments that contained tephra or silt and clay with less than 2% organic carbon (Fig. 4). The 200 *Betula* grains that were measured for species identification had an average diameter and standard deviation of 20.43 ± 1.41 μm and pore size of 2.55 ± 0.12 μm. *B. papyrifera* diameters measured by Ives (1977) and Clegg et al. (2005) were 28.78 ± 1.26 μm and 23.03 ± 3.11 μm, respectively, while *B. glandulosa* diameters measured by the same studies were 23.99 ± 1.82 μm and 20.71 ± 2.35 μm, respectively. Based upon these results, we conclude that the *Betula* pollen identified at Star Meadows is most likely *B. glandulosa*.

3.3.1. Zone SM 5e (809–751 cm; ca. 125–116 ka; 15 pollen samples)

This zone is distinguished by having the highest percentages of *Pinus* (60–90%) in the core. The remainder of the arboreal taxa consists of minor amounts of *Picea* (2–6%), *Abies* (2–6%), *Pseudotsuga/Larix*-type (1–5%), *Alnus* (2–10%), and *Betula* (0–2%). Other minor components include *Salix* (detected in the uppermost sample), *Sarcobatus* (0–1%), Ericaceae (0–1%), Rosaceae (0–1%), *Arceuthobium* (0–1%), and *Artemisia* (1–6%). The herbaceous taxa consists of Poaceae (0–9%) and very minor amounts of members of the Asteraceae family (*Ambrosia*-type 0–1% and Tubuliflorae 0–1%), and Amaranthaceae (0–1%). The aquatic pollen types represented include highly variable amounts of Cyperaceae (4–55%), *Nuphar* (only detected in the bottom-most sample), and Typhaceae (only in the top sample of this zone). *Pediastrum* (0–6%) abundance decreases towards the top of the zone, while *Botryococcus* varies greatly (1–24%).

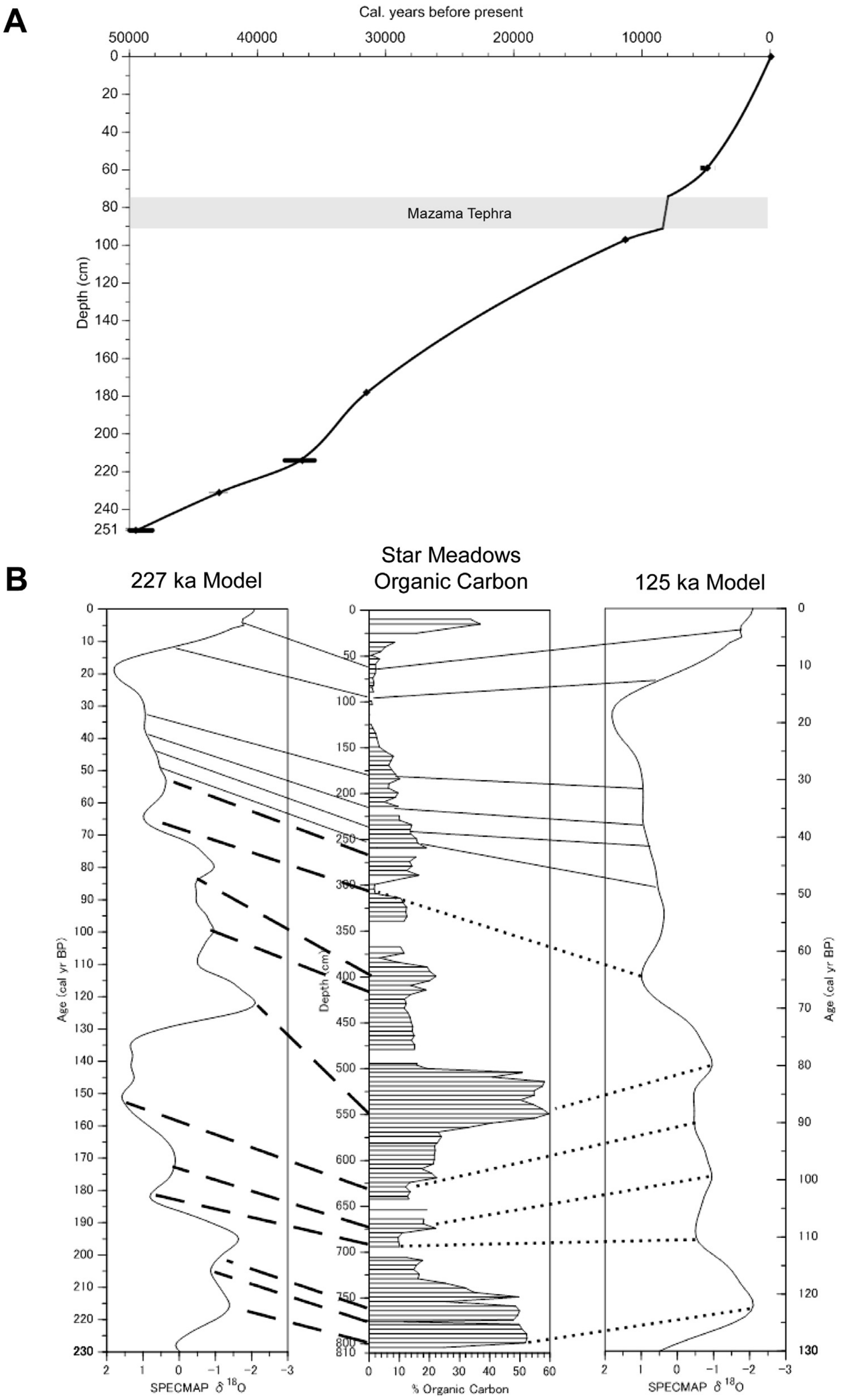

Fig. 3. (A) Age–depth relationship of the top 251 cm of the Star Meadows core based on six AMS ^{14}C dates and the Mazama tephra (ca. 7.63 ka). (B) Comparison of the 227 ka and 125 ka age models using δ^{18}O SPECMAP (Imbrie et al., 1984) curve and percent organic carbon curve from Star Meadows.

3.3.2. Zone SM 5d–5b (751–553 cm; ca. 116–84 ka; 48 pollen samples)

This zone stands out from the other pollen zones because both *Pseudotsuga/Larix*-type (2–18%) and *Betula* (0–9%) increase substantially. The remainder of the arboreal component consists of *Pinus* (37–87%), *Picea* (0.5–15.5%), *Abies* (2–7%), and *Alnus* (1–5%). *Salix* (trace levels), *Sarcobatus* (0–2%), Ericaceae (0–2%), Rosaceae (0–2%), *Arceuthobium* (0–1%), and *Artemisia* (1–6%) make up the

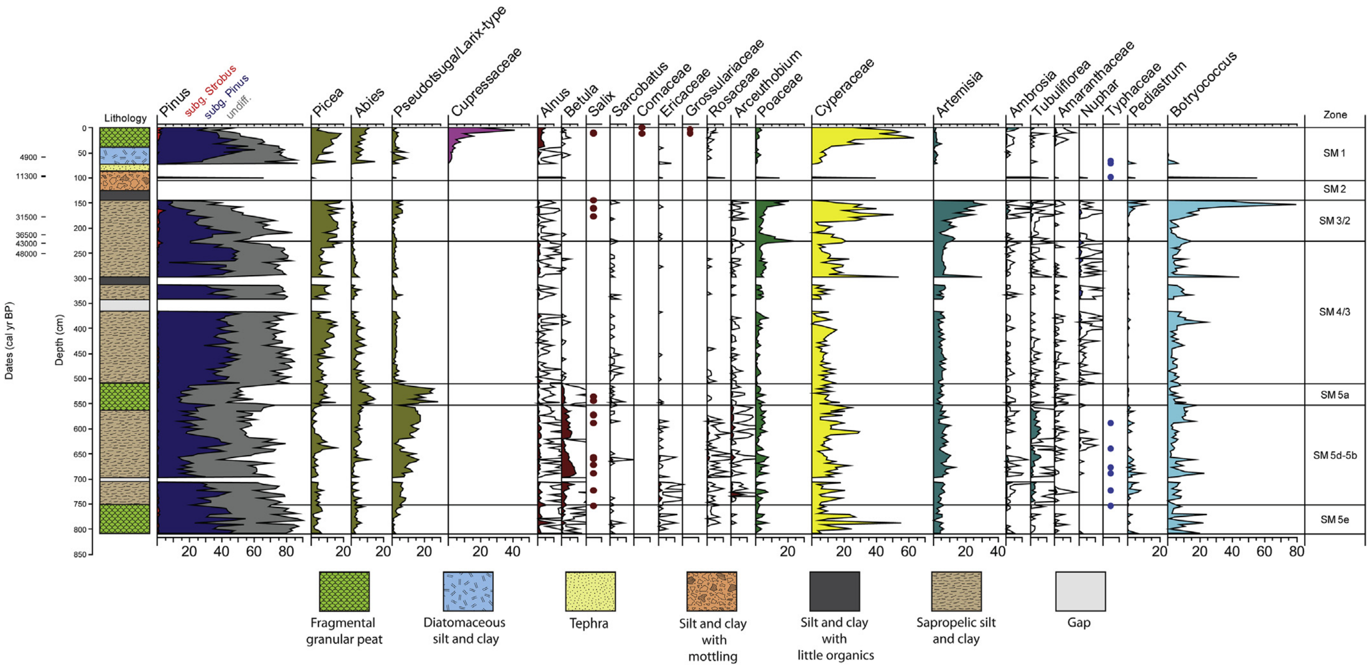

Fig. 4. The pollen record from Star Meadows, Idaho. Presence of *Salix*, Cornaceae, Grossulariaceae, and Typhaceae are show by circle symbols. Black lines for *Alnus*, *Betula*, *Sarcobatus*, Ericaceae, Rosaceae, *Arceuthobium*, *Ambrosia*-type, Tubuliflorae, Amaranthaceae, and *Nuphar* indicate 10× exaggeration.

remainder of the pollen taxa of woody plants. Poaceae (0–9%) and Tubuliflorae (0–6%) dominate the herbaceous taxa, while *Ambrosia*-type (0–1%) and Amaranthaceae (0–1%) are minor components. Cyperaceae (4–30%) and Typhaceae (trace levels) can be found throughout the zone, while *Nuphar* (0–1%), is present mainly in the middle of this zone. *Pediastrum* (0–10%) and *Botryococcus* varies greatly.

3.3.3. Zone SM 5a (553–510 cm; ca. 84–71 ka; 5 pollen samples)

This zone has the highest percentage of *Pseudotsuga/Larix*-type (4–28%) observed in the core. The remainder of the arboreal and shrub taxa include *Pinus* (43–73%), *Picea* (6–10%), *Abies* (5–12%), *Alnus* (1–5%), and *Betula* (0–3%). *Salix* (trace levels), *Sarcobatus* (0–1%), Ericaceae (0–1%), Rosaceae (0–1%), *Arceuthobium* (0–1%), and *Artemisia* (0–1%) comprise other woody taxa. The herbaceous component consists of Poaceae (0–5%), *Ambrosia*-type (0–1%), Tubuliflorae (0–1%), and Amaranthaceae (0–1%). Cyperaceae (2–17%) dominates the aquatic taxa, while Typhaceae and *Nuphar* are absent. *Pediastrum* (0–1%) and *Botryococcus* (1–8%) are minor components.

3.3.4. Zone SM 4/3 (510–225 cm; ca. 71–40 ka; 64 pollen samples)

This is the largest zone and is dominated by *Pinus* (40–84%) and *Picea* (4–18%). *Abies* (0–8%), *Pseudotsuga/Larix*-type (1–7%), *Alnus* (0–3%), and *Betula* (0–1%) comprise the remainder of the arboreal and shrub pollen. *Salix* is absent, while *Sarcobatus* (0–1%), Ericaceae (0–1%), Rosaceae (0–1%), and *Arceuthobium* (0–1%) are all present as minor components. *Artemisia* varies little within this zone (3–11%) with the exception of a single sample of 30% at 297 cm. Poaceae (0–25%) dominates the non-arboreal taxa and increases towards the top of this zone. *Ambrosia*-type (0–1%), Tubuliflorae (0–2%), and Amaranthaceae (0–1%) comprise the remainder of herbaceous component. Cyperaceae (2–23%) is highly variable within the zone with a large peak (55%) occurring at 297 cm. *Nuphar* (0–3%) is consistently present. There is very little *Pediastrum* (0–2%) and variable amounts of *Botryococcus* (3–24%), with a peak (43%) occurring at 287 cm.

3.3.5. Zone SM 3/2 (225–144 cm; ca. 40–22.8 ka; 20 pollen samples)

The highest percentages of *Picea* (8–19%) occur within this zone. *Pinus* (40–82%) declines in abundance towards the top of this zone, while *Abies* (0–3%), *Pseudotsuga/Larix*-type (0–7%), and *Alnus* (0–1%) are not major components of the arboreal taxa. *Betula* is only detected as one grain near the base of this section. Other woody taxa within this zone are *Salix* (detected only in the upper half of the zone), *Sarcobatus* (0–1%), Ericaceae (0–1%), and *Arceuthobium* (0–1%). *Artemisia* (4–30%) increases dramatically towards the top of this zone. Poaceae (2–24%) decreases at the base of this zone and then increases towards the top. The remainder of the non-arboreal taxa consists of *Ambrosia*-type (0–3%), Tubuliflorae (0–2%), and Amaranthaceae (0–1%). Cyperaceae (3–50%) pollen is highly variable throughout this zone and increases towards the top. *Nuphar* (0–3%) is detected at the base and top of the zone, while Typhaceae is not detected. *Pediastrum* (0–12%) and *Botryococcus* (1–80%), have their highest percentages of the entire core occurring at the top of this section.

3.3.6. Zone SM 2 (144–105 cm; ca. 22.8–14 ka)

The pollen concentration within this zone was too low and degraded (less than 7000 grains/cm^3) to complete pollen counts. For example, at a depth of 106 cm (ca. 14.5 ka), a total of 89 pollen grains could be identified with significant effort. Of these 89 grains, 53 were *Artemisia* while most of the remainder were fragments of *Pinus*.

3.3.7. Zone SM 1 (105–0 cm; ca. 14 ka to present; 23 pollen samples)

The pollen concentration was too low to complete any pollen counts through much of the Pleistocene to Holocene transition at the base of this zone. One sample of early-Holocene age contained sufficient identifiable pollen, marked by high percentages of *Pinus* (58%), Poaceae (15%), and *Ambrosia*-type (7%). The remainder of the samples represent the mid to late Holocene vegetation, distinguished by the first appearance of Cupressaceae (most likely *T. plicata*) pollen. Cupressaceae pollen first appears at 67 cm and increases in an exponential fashion towards the top (to a maximum of 41%). The uppermost samples also contain the first appearance of Cornaceae and Grossulariaceae. The rest of the arboreal taxa consist of *Pinus* (49–87%), *Picea* (2–20%), *Abies* (1–15%), *Pseudotsuga/Larix*-type (1–9%), *Alnus* (0–5%), and *Betula* (0–1%). *Salix* is detected in one sample near the top of the core. Ericaceae (0–1%) is detected only at two depths, while Rosaceae (0–1%) increases slightly towards the top. *Arceuthobium* is not detected while *Artemisia* varies little (0–5%) with the exception of a single sample of 15% at 99 cm. Non-arboreal taxa consist of *Ambrosia*-type (0–1%), Tubuliflorae (0–1%), and Amaranthaceae (0–1%). Cyperaceae pollen varies greatly from 4 to 65% with the highest abundance occurring at the top of the core. *Nuphar* (0–1%) is only present at 99 cm, while Typhaceae is detected in the lower half of this zone. Percentages are relatively low for both of the algae taxa *Pediastrum* (0–5%) and *Botryococcus* (0–55%) and are only detected in the lower half of the zone.

4. Discussion

In the discussion that follows, we show that there is a strong correspondence between the CONISS pollen zones and the lithological profile, and thus that there were parallel changes in upland vegetation and the wetland environment as controlled by water levels. The combined lines of evidence support a qualitative interpretation of vegetation and climate (Fig. 5). The most recent modern pollen spectra database (Whitmore et al., 2005) contains too few samples in the Northern Rocky Mountains, thus precluding a quantitative modern analog analysis.

4.1. Zone SM 5e (809–751 cm ca. 125–116 ka)

This sediment in this zone is comprised of dense fragmented granular peat with low bulk density and high organic carbon percentages. Vegetation within the meadow was dominated by *Carex*. The meadow was wet periodically as algae were rare (*Pediastrum*) or intermittent (*Botryococcus*), *Nuphar* was mostly absent, and biogenic silica was low (<3%). The meadow was lined with wetland taxa including *B. glandulosa*, *Salix*, and *Alnus* (Fig. 5). We interpret the pollen assemblage as representing a forest dominated by *P. contorta*, with minor components of *P. engelmannii*, *A. lasiocarpa*, *Pseudotsuga* and/or *Larix*, and Ericaceae (likely *Vaccinium* shrubs). The dominance of *Pinus* and the low lake levels at this time indicates that the climate was warmer and drier than at Star Meadows today.

4.2. Zone SM 5d–5b (751–553 cm; ca. 116–84 ka)

The sediment in this zone is a stiff sapropelic silt and clay consistent with a lacustrine origin. Water levels rose within the meadow forming a wetland that was able to support *Nuphar*. The presence of *Nuphar* and persistence of high biogenic silica indicates that the site never dried and maintained a lake level of at least a 0.5 m (Gaillard and Birks, 2013). Bog taxa, such as Typhaceae, *Salix*, *B. glandulosa*, Cyperaceae, and possibly *Comarum palustre* (Rosaceae) persisted around the margin of the lake. *Pinus* (likely *P. contorta*), *P. engelmannii*, and *Larix occidentalis* and/or *P. menziesii* form most of the forest composition with minor amounts of *Arceuthobium* in the tree canopy and herbaceous taxa (Poaceae, *Ambrosia*-type, and Tubuliflorae) constituting the understory. The forests during this period of time may represent a mixed conifer Douglas-fir forest surrounding the cool-adapted wetland shrub *B. glandulosa*. This vegetation, and the high lake levels, indicate that the climate in the Star Meadows region was cooler than what is found today.

4.3. Zone SM 5a (553–510 cm; ca. 84–71 ka)

Several factors including lithology (fragmented granular peat), high C:N, low biogenic silica, absence of *Nuphar* (only one grain detected at the base of this section), and low abundance of algae indicate that the wetland dried out and supported a sedge meadow. The forest surrounding the meadow remained similar to forest described during MIS 5d–5b. *Pseudotsuga* and/or *Larix* are the dominant forest taxon with minor amounts of *Picea*, *Abies*, and *Pinus* (likely *P. contorta* and/or *P. monticola*, which are both found in the region today). The abundant *Pseudotsuga* or *Larix*, decreasing amount of *Betula*, and lack of aquatic taxa indicate that climate was slightly warmer and drier than the previous time period (MIS 5d–5b) but remained sufficiently moist to maintain a wetland.

4.4. Zone SM 4/3 (510–225 cm; ca. 71–40 ka)

The lithology of this zone is mainly comprised of a sapropelic layer interrupted by a short segment of silt and clay containing little organic content from 300 to 314 cm. Relatively high abundances of biogenic silica along with the presence of *Nuphar* throughout most of this section suggests that 0.5–3 m of standing water persisted in the meadow (Gaillard and Birks, 2013). Most of the wetland taxa such as *Betula*, Typhaceae, and *Salix*, which were detected in during MIS 5d–5b and slightly in SM 5a are no longer present during this time. *Pinus* (likely *P. contorta*) and *P. engelmannii* are the dominant trees of the forest while *Pseudotsuga* or *Larix trees* and *Abies* (likely *A. lasiocarpa*) were only minor components. The pollen assemblage, especially the high *Picea* percentages, suggest the forest was a montane spruce forest (cold winters and moderately short mild summers) such as occurs at mid-to-high elevations in northern Idaho today.

The peak that occurred in bulk density and magnetic susceptibility with a corresponding trough in percent organic carbon and biogenic silica at 300–314 cm most likely represents a glacial advance. The inorganic sediment and lack of pollen preservation in this section suggests a major decline in vegetation cover and an increase in silt deposition. Our estimated age of this event (60–70 ka) is consistent with an extreme stadial event, Heinrich event H6 at 66 ka, during MIS 4 (Bond et al., 1992; Rashid et al., 2003; Hemming, 2004; McDonald et al., 2012). West of the study area, in eastern Washington, loess stratigraphy indicates major glacial outburst flooding associated with Cordilleran ice advance at this time (McDonald et al., 2012). The first pollen assemblage following this period has very high (30%) *Artemisia* pollen. The cool temperatures during this ice sheet advance would have caused the tree line to lower, increasing *Picea* and *Pinus* abundances at lower elevations, and *Artemisia* at higher elevations.

4.5. Zone SM 3/2 (225–144 cm; ca. 40–22.8 ka)

This zone is comprised of a sapropelic silt and clay layer with low percent organic carbon, increasing bulk density, and decreasing biogenic silica. *Nuphar* and algae present throughout most of this period indicate the continued presence of a lake that was surrounded by wetland taxa (*Salix* and *Carex*). The forest surrounding the wetland was dominated by *Pinus* and *Picea* with both *Abies* and *Pseudotsuga* or *Larix trees* present as minor components, similar to the forest composition of SM 4/3. *Pinus* decreases at the beginning

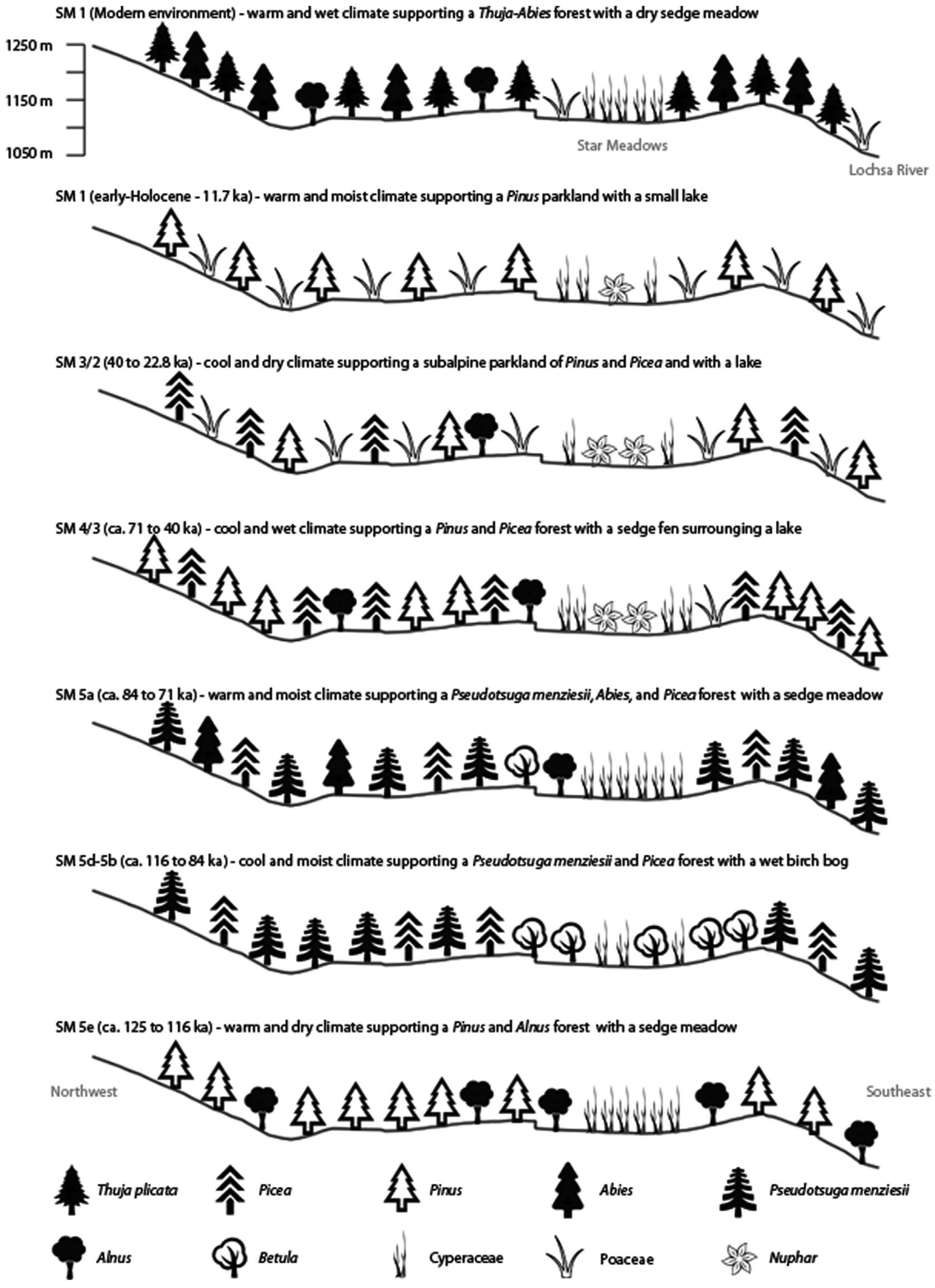

Fig. 5. Schematic transects across Star Meadows showing the dominant vegetation, based on the pollen record, for each pollen zone with the exception of SM-2.

of this time period as *Artemisia* and herbaceous taxa (Poaceae, *Ambrosia*-type, Tubuliflorae, and Amaranthaceae) increase in abundance. These changes in the pollen assemblage indicate the establishment of an open environment, possibly marked by lowering of tree line and the expansion of *Artemisia* at higher elevation. The climate was likely becoming significantly colder and possibly drier (but not enough to greatly lower water depth at the core site) into the LGM.

4.6. Zone SM 2 (144–105 cm; ca. 22.8–14 ka)

This zone is marked by stiff silt and clay with very little organic material, low pollen concentration, and dominance of *Artemisia* pollen (>60%) in the one sample where pollen could be identified. This suggests the region had low tree cover and a very short growing season. This is consistent with a pollen record from Lost Trail Pass Bog in the Bitterroot Range (Mehringer et al., 1977) that was interpreted to reveal a vast treeless landscape during the Lateglacial period.

4.7. Zone SM 1 (105–0 cm; ca. 14 ka to present)

There was sufficient organic matter during the early Holocene period for only one pollen sample (99 cm; ca. 11.7 ka). A small lake occupied the site, as indicated by the presence of *Nuphar*, and the lake was productive enough for algae (*Pediastrum* and *Botryococcus*) to occur in high abundances. Cyperaceae and Typhaceae were the dominant wetland taxa surrounding the lake. A forest dominated by *Pinus*, with a few *Picea* and *Pseudotsuga* or *Larix* trees occurred around the lake with an understory containing high abundances of herbaceous taxa (Poaceae, *Ambrosia*-type and Tubuliflorae) indicating an open warm-dry habitat.

The pollen assemblages post-dating the Mazama tephra (ca. 7.63 ka) are very different from any previous assemblage. The absence of *Nuphar* and low algae abundances in this portion of the core, indicates that the lake dissipated and a wet sedge meadow established. This was likely more the result of the basin filling with sediment (to within 20 cm of the sill as determined by LIDAR data) rather than climatic drying. Within the meadow, *Carex*, *Salix*, and *Comarum palustre* constitute the wetland vegetation. The forest surrounding the meadow is increasingly dominated by *T. plicata,* with minor amounts of *P. monticola*, *P. engelmannii*, *A. grandis*, *P. menziesii*, and *Alnus*. Cornaceae and Grossulariaceae (likely *Ribes*) also make their first appearance in the pollen record near the top of this section. *T. plicata*, Cornaceae, and *Ribes* are currently associated with the warm and wet climate of the mesic forests.

4.8. Comparison of the Star Meadows record with other long records in western North America

Our knowledge of past climate and vegetation over long time scales has vastly improved over the last several decades due to newly developed high-resolution pollen records. Some of these terrestrial sediment records extend back to the previous interglacial or even further back in time. In western North America, there are only a few continuous high-resolution terrestrial sediment records that extend back to the Last Interglacial period (120 ka) and even fewer of these records are age constrained. In Fig. 6 we present three long continuous terrestrial pollen records from western North America that have both climate and vegetation interpretations: Carp Lake (Whitlock and Bartlein, 1997; Whitlock et al., 2000), Humptulips (Heusser et al., 1999), and Bear Lake (Jiménez-Moreno et al., 2007). Additional sites that provide records of MIS 5 (Ziegler Reservoir Site, Colorado (Anderson et al., 2014)) and MIS 2 and 3 (Fargher Lake, Washington (Grigg and Whitlock, 2002) and Little Lake, Oregon (Grigg et al., 2001)) were included in our comparison.

These records reveal broad similarities of millennial-scale insolation-driven changes in vegetation, and responses to glacial maxima. For example, both Bear Lake on the Idaho–Utah border and Star Meadows show peaks in warm and dry indicators during MIS 5e and colder indicators consistent with a significantly lower treeline during MIS 2 (Jimenez Moreno et al., 2007). In addition, both Bear Lake and Star Meadows show evidence of response to Heinrich events, especially H6, providing further support that these events were of sufficient magnitude and duration to affect regional vegetation (Jimenez Moreno et al., 2007). However, there are also many minor differences in the vegetation histories that may stem from spatial variation in climate change or the ecological responses to climate change. For example, topography and the development of microclimates likely play an important role in determining climate at a local or extralocal scale of individual sediment records (Dobrowski, 2011). In addition, differences in pollen source areas and difficulties in dating beyond the limit of radiocarbon hinder inter-site comparisons. Large lakes such as Bear Lake reflect regional patterns of vegetation, while small lakes such as Carp Lake (Whitlock and Bartlein, 1997; Whitlock et al., 2000), show vegetation at a more local scale.

During MIS 5e, the climate at Star Meadows was warm and dry, which is consistent with other pollen records in western North America, including but not limited to Carp Lake (Whitlock and Bartlein, 1997; Whitlock et al., 2000), Bear Lake (Jiménez-Moreno et al., 2007), and Ziegler Reservoir (Anderson et al., 2014). Climate cooled and moisture increased at Star Meadows during MIS 5d–5b. A similar trend has been observed at Ziegler Reservoir, Carp Lake, and Bear Lake, each with alternating temperature regimes among MIS 5b, 5c, and 5d (with MIS 5b surprisingly cold at Ziegler, Anderson et al., 2014). Unlike these sites, MIS 5d, 5c, and 5b could not be easily separated in our record. At Star Meadows, MIS 5a was a period of warm and moist conditions which is similarly observed at Humptulips, transitioning to drier conditions near the MIS 5a to MIS 4 transition (Heusser et al., 1999). In addition, a warm MIS 5a was identified at Carp Lake (with wetter conditions), Bear Lake (with arid conditions), and Ziegler Reservoir. At Clear Lake, California, MIS 5a and 5c were the warmest intervals during MIS 5 (Adam et al., 1981).

With the onset of MIS 4 and into MIS 3 (ca. 71–40 ka), the area around Star Meadows became cool and wet. The pollen record suggests that the vegetation was stable throughout this period. The transition into MIS 3 was not detected at Star Meadows. Other long cores in western North America show a similar cooling trend but also more variations in climate and vegetation during this time (Fig. 6). Fargher Lake, Washington (Grigg and Whitlock, 2002) and Little Lake, Oregon (Grigg et al., 2001), indicate a cool and mostly wet climate persisted during most of MIS 3. The climate and vegetation in the Star Meadows area continued to remain cool and wet during MIS 3 and the beginning of MIS 2 (ca. 40–22.8 ka) with the only notable changes in vegetation consisting of a decrease in *Pinus* and increases of *Picea,* Poaceae, Cyperaceae, and *Artemisia*. The record from Bear Lake also shows cool and moist conditions throughout this period and into MIS 2. At Carp Lake and Humptulips, cold and dry conditions persisted from the onset of MIS 3 and throughout to MIS 2, with the exception of warm and dry conditions occurring at Carp Lake at 13.2 ka. The climate and vegetation records from Little Lake, Fargher Lake, and Kalaloch, Washington (Heusser, 1972) all suggest that climate remained cool, but became drier during MIS 2 (Grigg and Whitlock, 2002). The record from Clear Lake indicates that the climate was cool to cold during MIS 2, 3, and 4. The remainder of MIS 2 at Star Meadows did not yield pollen, but increasing *Artemisia* into the LGM and low organic content suggest periglacial conditions. All records show a sharp warming trend and rapid vegetation shifts at the start of MIS 1.

Star Meadows appears to have remained wet throughout the majority of the record, with the exception of the dry period at the base of the core, the extreme stadial within SM 4/3, and for the entire LGM within SM 2. This finding is in contrast with the other three records which all experienced drier climates more frequently. While qualitative interpretations from pollen assemblages have limited power, the first impression from this comparison (Fig. 6) is consistent with higher moisture conditions persisting through the late Pleistocene in the mountains of northern Idaho compared to other areas.

4.9. Late-Holocene arrival of the mesic forests in northern Idaho

If a mesic forest environment persisted during the last glaciation within a refugium in the Clearwater drainage, as previous

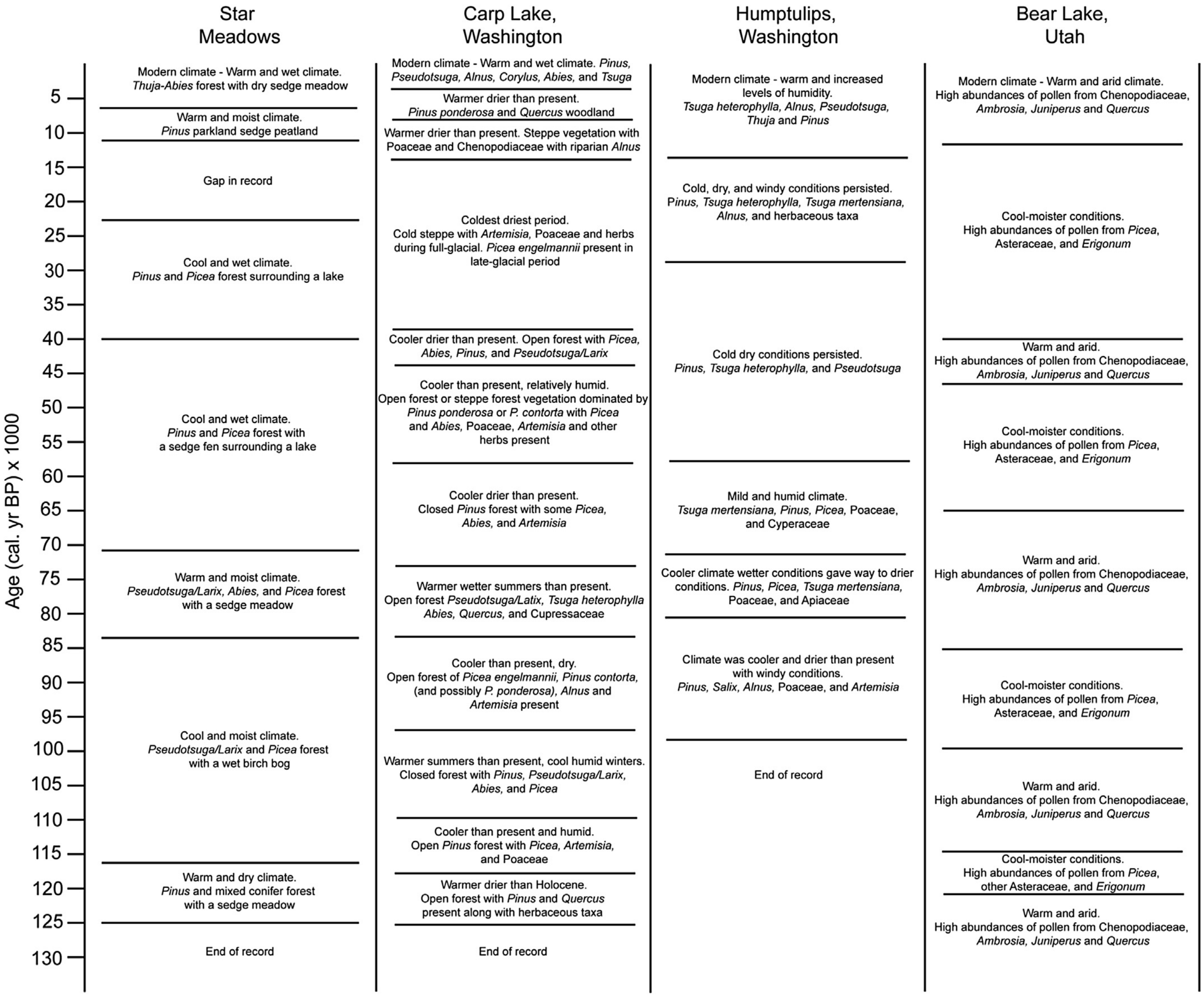

Fig. 6. Comparison of climate and vegetation between the Star Meadows record and select long records in western North America including Carp Lake, Washington (Whitlock and Bartlein, 1997; Whitlock et al., 2000), Humptulips, Washington (Heusser et al., 1999), and Bear Lake, Utah (Jiménez-Moreno et al., 2007).

phylogenetic research has suggested (i.e. Brunsfeld and Sullivan, 2005; Brunsfeld et al., 2007; Carstens and Richards, 2007), then indicators of a mesic environment (i.e. mesic taxa) similar to the late-Holocene would be present prior to the onset of Holocene. Although much of the last 120,000 years the landscape around Star Meadows was forested, we found two periods during the late Pleistocene with extremely low forest cover, challenging the possibility that a mesic refugium could have existed continuously in the broader region. Furthermore, the taxa most strongly associated with mesic climate, *T. plicata*, first appears in the pollen record only at ca. 6.3 ka. Below we discuss this history of *T. plicata* and its implications for understanding the existence of a mesic refugium in northern Idaho.

The mid-Holocene arrival of mesic taxa in northern Idaho is consistent with other paleorecords from glaciated areas in the Columbia Mountains of British Columbia. At Lower Slocan Lake, *T. plicata* appears in the paleorecord at approximately 5 ka (Hebda, 1995) and at Mirror Lake (Kaslo, BC) at 3 ka (Gavin, unpublished data). *T. plicata* can often be found in association with *Tsuga heterophylla* throughout most of its current distributions. However, the modern distribution of *T. heterophylla* does not extend south to the Lochsa River. Further north in Idaho and British Columbia, paleorecords provide evidence that *T. heterophylla*, like *T. plicata*, is a relatively recent arrival to the interior mesic forests. In northern Idaho near Priest Lake *Thuja–Tsuga* forests increased in abundance at 2.5 ka (Mehringer, 1985, 1996), while farther north in British Columbia these species increased in abundance (>2%) after ca. 4 ka (Gavin et al., 2006).

The increase in abundance of *T. plicata* over the last ca. 6.3 ka shows that the forests during the late-Holocene were different than any other forest that existed in the Holocene and previous interglacial. What was different about the Holocene that enabled the establishment and later dominance of *T. plicata* and other mesic taxa in the region? We propose three main hypotheses for why mesic taxa, including *T. plicata*, did not establish in northern Idaho until the mid-Holocene. The relatively recent arrival of mesic taxa could have been limited by 1) dispersal, 2) climate, and/or 3) conditions for seedling establishment.

The first two explanations for the Holocene appearance of mesic taxa are that they were dispersal-limited due to a >100 km wide arid barrier between their main coastal populations and the northern Rocky Mountains, or that climate was not suitable for the mesic taxa prior to the Holocene. If dispersal was the only factor limiting the distribution of certain mesic taxa during the Holocene, then it can be assumed the past climate could have supported other mesic taxa. Comparison within the core between MIS 1 (SM 1, modern environment) and MIS 5 (SM 5e through SM 5a) shows that the vegetation and climate during these two time periods were not similar. Other than the recent occurrence of Cupressaceae, the most notable difference between the two time periods is the high abundances of *Betula* and *Pseudotsuga/Larix* during MIS 5, whereas both taxa are found in low abundances in the modern landscape (MIS 1). *B. glandulosa* and *T. plicata* can be found in association with one another today, but are always found in association with *Tsuga heterophylla* and at higher latitudes in a cooler environment, such as at the north end of Priest Lake in the Selkirk Mountains (Chadde et al., 1998). Like Star Meadows, the records from Carp Lake (Whitlock and Bartlein, 1997; Whitlock et al., 2000), Humptulips (Heusser et al., 1999), and Bear Lake (Jiménez-Moreno et al., 2007) all show somewhat warmer temperatures existed during MIS 5e and cooler temperatures during other substages of MIS 5. The warm and moist summers that characterize interior mesic forests may have not existed during MIS 5. This is consistent with other studies that concluded that MIS 5 is not a good analog for the current interglacial (Loutre and Berger, 2003; McManus et al., 2003). Instead, MIS 11 is a better analog for the Holocene because of its similar orbital configurations, carbon dioxide and other greenhouse gas concentrations, and because it represents the longest and warmest interglacial (similar to the Holocene) in the last 500 ka (Muller and MacDonald, 1997; Raynaud et al., 2005). The early Holocene was also likely too warm and dry for *T. plicata* forests, instead supporting a *Pinus* parkland (Fig. 5). Modern climate is cooler and wetter than the early Holocene, suggesting that climate prior to the mid-Holocene was not ideal for mesic taxa expansion into the region. Thus, the regional vegetation history is more consistent with a climatic limitation, rather than dispersal limitation, affecting the Holocene establishment of *T. plicata* forests. Many other associated mesic-adapted taxa may have been affected similarly.

Although climate at Star Meadows may have been unsuitable for *T. plicata* (and possibly other mesic-adapted species) before the Holocene, the pollen data can not resolve whether most or all mesic-adapted taxa were restricted to the coast or whether they may have existed in the northern Rocky Mountains in small isolated refugia. The phylogeography of *Cardamine constancei*, an herbaceous species associated with *T. plicata* and endemic to northern Idaho, indicates small populations persisted within separate river canyons in unglaciated areas in northern Idaho (Brunsfeld and Sullivan, 2005). During the LGM (MIS 2), however, almost no pollen was recovered (SM 2). The climate of the LGM and Lateglacial was probably extremely challenging for mesic-adapted taxa in the region, as high levels of *Artemisia* suggest a very low tree line and a very short growing season. Our record, therefore, challenges the inference from genetics and patterns of endemism of the persistence of a mesic refugium existing in the region during the LGM (Gavin et al., 2014). The LGM period presents the largest hurdle for the persistence of mesic-adapted taxa in an interior refugium.

Species distribution models of several species (i.e. *Ascaphus montanus*, *Plethodon idahoensis*, *Microtus richardsoni*, *Salix melanopis*, *T. plicata*) residing within the interior mesic forests show that the LGM climate was too harsh for many of the species currently found in the region today (Carstens and Richards, 2007; Roberts and Hamann, 2015). Both vegetation (subalpine *Pinus* and *Picea* forest with high abundances of *Artemisia*; SM 3/2) and sediment composition records (low percent organic carbon, decreasing biogenic silica, and increasing bulk density; SM 3/2 and SM 2) support climate simulations of a cold and dry LGM (Braconnot et al., 2007). In order to test if small isolated pockets of suitable climate could have existed in the region during the LGM, topographic effects on climate needs to be assessed throughout the mountains. Alternatively, there are many canyons further south of Star Meadows. Perhaps a refugium for mesic-adapted species was able to exist on south facing slopes in a region south of Star Meadows.

A third possibility that may have promoted the Holocene arrival of *T. plicata* in northern Idaho was the tephra deposited from the eruption of Mt. Mazama. A total of 17 cm of ash was preserved in the Star Meadows core, which is consistent with other records in northern Idaho (e.g. Mehringer et al., 1977; Shipley and Sarna-Wojcicki, 1983; Matz, 1987; Brunelle and Whitlock, 2003; Kimsey et al., 2007). In paleorecords recovered in Oregon, the Mazama tephra has had a profound effect on vegetation by increasing the non-arboreal component in the ecosystem following ash deposition (Long et al., 2011, 2014). Similar to the sites in Oregon, the deposition of a thick Mazama ash at Star Meadows may have suppressed competing vegetation and mulched soils thereby increasing soil water capacity and enabling mesic taxa such as *T. plicata* to establish and increase in abundance fairly quickly. *T. plicata* is able to grow on nutrient-poor soils, and influences surrounding soils by raising pH and increasing soil cation capacities (Franklin et al., 2000). It is not known how well *T. plicata* germinates on ash relative to other species, but it may have been able to outcompete other forest taxa that are not able to establish as easily on ash. For this hypothesis to be true, *T. plicata* must have already been present in the region to be a component of the seed bank prior to the deposition of tephra or seeds were frequently dispersed from the coast to the interior regions. In order to test this hypothesis, germination studies for *T. plicata* and other tree taxa need to be conducted on Mazama ash.

5. Conclusion

The Star Meadows core provides us our first glimpse of the climate and vegetation history in northern Idaho over the last ca. 120 ka. The pollen record suggests that the region underwent several major vegetation changes as a response to shifts in climate at millennial scales. Pollen assemblages and sediment composition records can be linked to marine isotope stages, indicating global-scale climatic fluctuations were manifested as distinct vegetation changes in northern Idaho. At the base of the core (MIS 5e) a warm-dry climate existed enabling the establishment of a dry-mixed conifer forest around a dry sedge (*Carex*) meadow. During MIS 5d–5b the landscape became moister allowing a *Pseudotsuga/Larix* and *Picea* forest to develop on the slopes surrounding a wet birch (*Betula*) bog. Climate warmed again in MIS 5a which led a drop in lake levels and the increase in *Pseudotsuga* or *Larix trees*, with *Picea* and *Abies* around a wet *Carex* meadow. During MIS 4 to MIS 2, a cool and wet climate developed in the region and was marked by a severe stadial event at ca. 65 ka. An increase in available moisture enabled the basin to fill with water and support *Nuphar*, while *Pinus* and *Picea* dominated the forest surrounding the lake. From ca. 40–22.8 ka, cooler and drier (than present) conditions prevailed, facilitating a subalpine parkland of *Pinus* and *Picea* to develop around a lake. Due to the low amounts of organic matter and poor preservation of pollen, we do not have a good record of the LGM at Star Meadows. Glaciers extended down-valley less than 10 km from Star Meadows, consistent with the evidence of sparse vegetation in the immediate region (Dingler and Breckenridge, 1982). During the early Holocene (11.7 ka), climate warmed facilitating a *Pinus* parkland dominated by Poaceae in the understory. The most dramatic change in vegetation occurred during the mid-Holocene with the appearance and then later dominance of *T. plicata* and other taxa associated with mesic forests in the region today.

The Holocene is a unique period due to the appearance and dominance of *T. plicata* over the last ca. 6.3 ka in the Star Meadows region. The recent arrival of mesic forest taxa suggests that their range may have been limited by dispersal, climate, or a combination of both. Recent dispersal from the coast is in agreement with phylogenetic studies conducted on *T. plicata* populations (O'Connell et al., 2008). Pollen and sediment composition records from the core suggests that climate of the Last Interglacial (MIS 5) did not support the summer warm-wet climate of the region today. Thus, climate may have been the primary limiting factor for both the initial establishment of *T. plicata* at any location in the interior and its absence at Star Meadows until the late Holocene. Under this interpretation, long distance dispersal from the coast could have occurred several times over the last 100 ka, but *T. plicata* was not able to colonize until a suitable climate was established during the Holocene. Pollen records, however, are unable to rule out earlier colonization of microrefugia in the interior, though given the interpretation of LGM climate at Star Meadows such sites were likely located to the south by hundreds of km. In addition, the eruption of Mt. Mazama could have aided in the establishment of the modern mesic forest by reducing competition and providing a good substrate for seedling establishment. The Star Meadows record challenges the notion that this region acted as a broad-scale mesic refugium during glacial conditions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2015.03.028.

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Supplementary Material

Fig. S1. Photos of the sediment core from Star Meadows, Idaho. Red marks are placed every 10 cm.