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A 15,000 year record of vegetation and climate change from a treeline lake in the Rocky Mountains, Wyoming, USA

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Abstract

Future climate projections predict warming at high elevations that will impact treeline species, but complex topographic relief in mountains complicates ecologic response, and we have a limited number of long-term studies examining vegetation change related to climate. In this study, pollen and conifer stomata were analyzed from a 2.3 m sediment core extending to 15,330 cal. yr BP recovered from a treeline lake in the Rocky Mountains of Wyoming. Both pollen and stomata record a sequence of vegetation and climate change similar in most respects to other regional studies, with sagebrush steppe and lowered treeline during the Late Pleistocene, rapid upward movement of treeline beginning about 11,500 cal. yr BP, treeline above modern between ~9000 and 6000 cal. yr BP, and then moving downslope ~5000 cal. yr BP, reaching modern limits by ~3000 cal. yr BP. Between 6000 and 5000 cal. yr BP sediments become increasingly organic and sedimentation rates increase. We interpret this as evidence for lower lake levels during an extended dry period with warmer summer temperatures and treeline advance. The complex topography of the Rocky Mountains makes it challenging to identify regional patterns associated with short term climatic variability, but our results contribute to gaining a better understanding of past ecologic responses at high elevation sites.

Keywords

climate change, conifer stomata, Holocene, pollen, Rocky Mountains, treeline, United States, Wyoming

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Introduction

Holocene records of vegetation and climate change in the Rocky Mountains of western North America record a history primarily controlled by long-term changes in insolation and the remnant effects of the continental ice sheets that altered temperatures, caused shifts in the latitudinal position of the jet stream, and affected the regional moisture balance (Bartlein et al., 1998; Brunelle and Whitlock, 2003; Fall, 1997; Fall et al., 1995; Whitlock, 1993). At local spatial scales, topographic controls increase in importance and orographic effects significantly influence precipitation patterns (Shinker, 2010; Whitlock and Bartlein, 1993). The Rocky Mountains are a region of complex topography with relatively few Holocene-length climate reconstructions, but a rapidly growing population that will be affected by possible changes in hydrology and water supply associated with potential future climate change (Shinker et al., 2010).

Shifts in the elevation of upper treeline are considered a sensitive indicator of climate change (LaMarche, 1973; Moir et al., 1999; Rochefort et al., 1994) and models of future climate predict upward movement of this boundary (Holtmeier and Broll, 2005). Analysis of treeline studies from across the globe found that treelines are advancing, but not universally. Within the Rocky Mountain region some sites were advancing, while others were stable (Elliott, 2011; Harsch et al., 2009). The variation in response to modern climatic warming underscores the need for more paleoecologic studies that improve our understanding of climate dynamics across the region.

Paleoecologic studies from long-term ecologic research sites provide an opportunity to compare past vegetation change with the current response to potential climate change. In this paper we present pollen and stomata data to reconstruct a 15,000 year record of vegetation and climate change from East Glacier Lake (EGL), a treeline lake in the Glacier Lakes Ecosystem Experiments Site (GLEES), a long-term ecologic research site. GLEES was established in an area that is wilderness-like, but not a federally mandated wilderness area. This means that research and instrumentation are allowed and can provide baseline and experimental data on relatively undisturbed alpine and subalpine ecosystems (Musselman, 1994). Meteorological data have been collected near GLEES since the late 1960s and a meteorological tower was constructed southwest of EGL in 1987 (Musselman, 1994). Trees have been invading meadows at the upper treeline in the Snowy Range in recent decades, indicating that this site may be sensitive to potential climate change (Moir et al., 1999); however this may be confounded by the removal of livestock in the 1990s after about a century of grazing. We compare our results with previous long-term studies of treeline change across the region.

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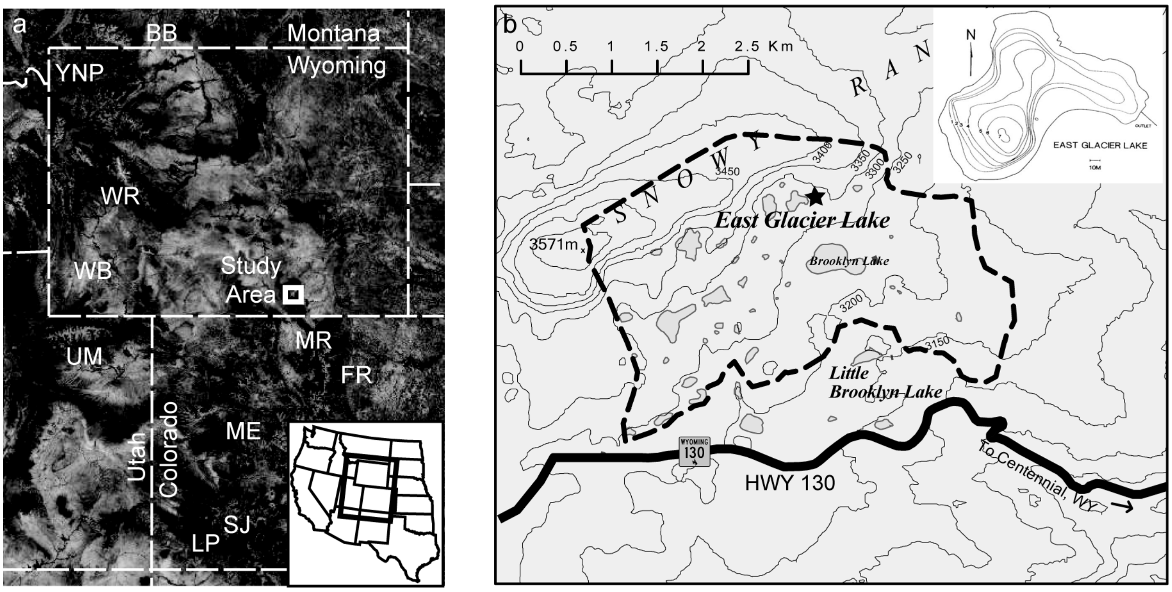

Figure 1. (a) Satellite image of the central Rocky Mountains including sites discussed in the text. BB: Bighorn Basin; FR: Front Range; LP: La Plata Mountains; ME: Mount Emmons; MR: Mummy Range; SJ: San Juan Mountains; UM: Uinta Mountains; WB: Wyoming Basin; WR: Wind River Range; YNP: Yellowstone National Park. (b) Map of study site with inset showing East Glacier Lake bathymetry using 1 m contours. Dashed line: Glacier Lakes Ecosystem Experiments Site boundary. Star: East Glacier Lake

Study area

EGL (elevation 3282 m) is at the upper treeline in the Snowy Range of the Rocky Mountains, a subrange of the Medicine Bow Mountains in southeastern Wyoming, USA (Figure 1). The lake has a maximum depth of 7.0 m, a surface area of 2.9 ha and watershed of 25.9 ha, most of which is unforested (Musselman, 1994). There is an outlet but no perennial inlet and nearly all of the hydrologic input is from surface runoff and groundwater. Flow from the outlet ceases after snowmelt is complete, usually by late August or early September. EGL receives all of its water from precipitation and does not have a permanent surface outflow, but percolates through glacial till and is likely subject to eutrophication when shallow.

The Snowy Range is 15 km in length, oriented southwest to northeast with a maximum elevation of 3661 m. The terrain includes periglacial features, tarns and numerous moraines. Geology in the Glacier Lakes Basin is predominantly quartzite with mafic dikes, schists and metaconglomerate lenses (Karlstrom and Houston, 1984; Rochette, 1994). Soils are thin, rocky, and contain large amounts of glacial till (Musselman, 1994). No carbonate soils are present within GLEES, but downstream in the watershed (2680 m elevation) the Nash dolomite, which contains minor amounts of carbonate, has produced some carbonate soils (Reider, 1983). Much of the lake's terrestrial sediment input results from aeolian transport (Finley and Drever, 1993).

Annual precipitation near the site for the period 1987–2002 (USDA Forest Service, unpublished data, 2003) averaged 121 cm, with 60–70% falling as snow, which can occur any month of the year. Precipitation is winter dominated with ~2.5 times as much falling during January through March as compared with July through September. Daily average temperatures range from −9.5°C in January to 11.7°C in July. Snow cover usually establishes by mid-October and persists until June with depths of ≥5 m in sheltered areas persisting into July. The prevailing northwest winds result in blowing snow accumulation in the lee of the ridge top just above East and West Glacier Lakes. The eastern escarpment of the Snowy Range harbors small permanent snowfields above 3300 m.

Vegetation consists of 'parkland' forest of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) (Regan et al., 1998), the dominant species between 3000 and 3300 m elevation (Dillon et al., 2005). Discontinuous spruce-fir forest occurs below 3250 m with large meadow areas and tightly clustered trees on higher, drier ground. Understory species in the spruce-fir forest are grouse whortleberry (*Vaccinium scoparium*) and marsh marigold (*Caltha leptosepala*) in wetter areas (Regan et al., 1998). Above the lake, grasses and forbs are dominant and tree species occur only in the form of krummholtz. Limber pine (*Pinus flexilis*) and common juniper (*Juniperus communis*) also occur infrequently near the lake. Lodgepole pine (*P. contorta*) is the dominant species at elevations of approximately 2400 to 3000 m (Dillon et al., 2005). Aspen (*Populus tremuloides*) and ponderosa pine (*P. ponderosa*) are much less common than in the Front Range to the south (Dillon et al., 2005). The primary source of forest disturbance at lower elevations is fire, although precise information on fire disturbance regime is not available (e.g., Billings, 1969; Brunelle and Minckley, unpublished data, 2010). Fires appear to occur infrequently at the higher elevations. Sedimentary charcoal analysis from Little Brooklyn Lake (Figure 1) indicates fire return intervals >1000 years (Brunelle and Minckley, unpublished data, 2010) and Billings (1969) estimated a return interval of 700 years at a similar site.

Methods

Core EGL-92-1 was collected by Jim Finley in 1992 during the winter when the lake was frozen, and placed in cold storage at the US Forest Service laboratory in Fort Collins, CO. In August 2005, the core was removed from storage and the three sections were thawed, split, described and then transported to the University of Nevada, Reno for analysis. Radiocarbon dating (see below) determined that the surface sediments were missing, and a second core (EGL-06-1) containing the upper 30 cm, including the sediment–water interface, was recovered in December 2006 using a plexiglass-piston corer. Sediments were sampled in the field in 1 cm contiguous intervals.

Chronology and sediment analysis

Five samples of organic sediment from EGL-92-1 and two from EGL-06-1 were submitted for AMS radiocarbon dating (Table 1).

Table 1. AMS radiocarbon ages obtained from two sediment cores, EGL-92-1 and EGL-06-1 (see text for coring details). All radiocarbon ages were calibrated using Calib 6.0. The median probability age of the 2-sigma range (rounded to the nearest decade) exported from Calib 6.0 was used to construct the age model

BetaLab #	Core	Depth (cm)	Material dated	^{14}C age	Error	Calib 2Σ min	Calib 2Σ max	Med. prob.
225057*	EGL-06-1	7	organic sed.	400	40	318	518	460
225058	EGL-06-1	25	organic sed.	980	40	794	958	870
216625*	EGL-92-1	9	organic sed.	1450	40	1295	1403	1340
216626*	EGL-92-1	59	organic sed.	4450	40	4882	5287	5100
216627*	EGL-92-1	75	organic sed.	5090	40	5743	5917	5820
216628*	EGL-92-1	154	organic sed.	9860	40	11,201	11,345	11,250
216629*	EGL-92-1	215	organic sed.	12760	40	14,890	15,583	15,140

* Dates used in the final age model.

No macrofossils were found for radiocarbon analysis. Results from these dates were used to match the two cores and create the final age model (described in results). All ages given in this paper are presented in calendar years before present (cal. yr BP), rounded to the nearest decade and were calibrated using CALIB 6.0 with the INTCAL09 calibration data set (Reimer et al., 2009). The median probability age for the 2-sigma distribution was used in constructing an age model (Telford et al., 2004). An age of −56 cal. yr BP was given to the surface sediment. All radiocarbon ages cited from the literature were recalibrated using the same method.

Samples (1.25 cc) were combusted at 550°C (LOI) to obtain the percent organic matter (Dean, 1974). A total of 35 samples were analyzed for organic content and pollen; 32 samples (~every 5–10 cm) from EGL-92-1 and 3 samples (0, 4 and 8 cm depth) from EGL-06-1.

Pollen and stomate analysis

Pollen preparation followed standard procedures (Faegri and Iverson, 1985). A known quantity of *Lycopodium* (clubmoss) spores was introduced into each sample for calibrating pollen concentration (Stockmarr, 1971). A minimum of 400 terrestrial pollen grains were counted from each sample. Of the 35 samples counted, 27 were counted by Mensing, and 8 were counted by both Mensing and Korfmacher. For samples counted by two researchers, each analyst counted a minimum of 200 terrestrial pollen grains from different slides and the results were combined to make a count of >400 grains. In all cases, percentages of major pollen types counted by the different analysts were comparable.

Pollen was identified to the lowest possible taxonomic level using reference material in the UNR Geography Palynology Lab and published pollen keys (Kapp et al., 2000; Moore and Webb, 1978). TCT pollen (Taxodiaceae, Cupressaceae, and Taxaceae) was assumed to be *Juniperus* (juniper), since no other genus of these three families occurs in the region.

Pollen percentages were calculated from the sum of terrestrial pollen and accumulation rates were calculated by dividing concentration by the number of years per sample. An index was calculated as a proxy for changes in treeline, using *Picea*, *Abies* and Poaceae. *Picea* and *Abies* are the dominant treeline species around EGL, while alpine tundra above treeline is dominated by Poaceae. We used the formula $[(p+a)-po] / [(p+a)+po]$ where p is percent *Picea*, a is percent *Abies* and po is percent Poaceae. Values approaching 1 represent high levels of *Picea* and *Abies* presuming trees at or above modern treeline, while values approaching −1 represent abundant grass, expansion of tundra, and lower treeline.

Aquatic pollen and algae were counted concurrently with terrestrial pollen, and are presented as accumulation rates since numbers of these types vary greatly throughout the record and abundance data represent their significance better than percentage data. Zonation was interpreted from a constrained single-link dendrogram created using a cluster analysis program modified from Birks and Gordon (1985); data input included the 16 most common taxa.

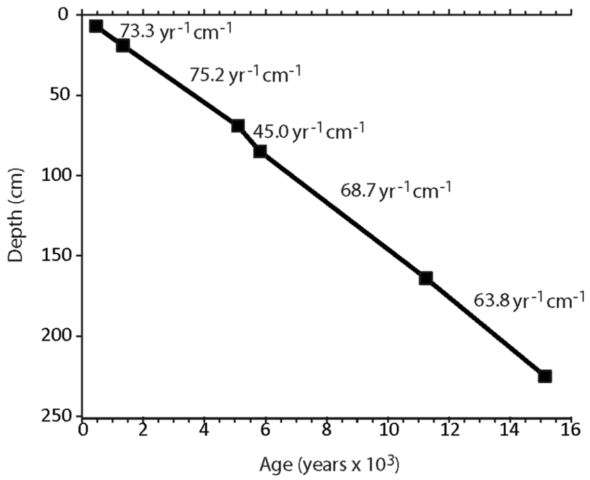

Figure 2. Age model. Solid line represents linear rate between calibrated radiocarbon ages listed in Table 1. Numbers are sedimentation rates between radiocarbon ages

Stomata can be used to determine the local presence of conifers in the absence of macrofossils (Hansen, 1995). Conifer stomatal guard cells can be identified on pollen slides, and during pollen analysis some cells were noted. Subsequent to counting pollen, three slides for each level were scanned at 100× magnification and all stomata were counted. Stomata were identified using UNR Geography Palynology Lab reference material, as well as published drawings (Hansen, 1995). *Lycopodium* control spores were counted on all pollen slides for calculating stomata accumulation rates.

Results

Chronology

Our age model used a simple linear age extrapolation between each radiocarbon date resulting in sedimentation rates of 73.7, 73.3, 75.2, 45.0, 68.7, and 63.8 yr/cm from the top to bottom of the core sections respectively (Figure 2). Thirty-seven samples were analyzed for pollen and the time between samples ranged from 150 to 750 years with the average being 450 years.

Three zones were identified from the cluster analysis: Zone 1 (15,330 to 11,500 cal. yr BP); Zone 2 (11,500 to 5200 cal. yr BP); and Zone 3 (5200 cal. yr BP to the surface). Zone 2 was further subdivided into three subzones: Zone 2A (11,500 to 9300 cal. yr BP) a transitional period in the early Holocene; 2B (9300 to 6000) a period with high abundance of subalpine conifers; and 2C (6000 to 5200 cal. yr BP) a period with low total pollen and stomata accumulation rates, high percentages of conifer pollen and percentage of organic carbon (Figures 3 and 4).

Sediments

Basal sediments (15,330 cal. yr BP) contain decomposed granite associated with deglaciation with 5% organic matter; lake sediments (gyttja) are present by 13,550 cal. yr BP. Percent organic matter varies little over the record, remaining between 20 and 30% throughout the core, except for Zone 2c when percent organics increased to 40% (Figure 3). The sediment is visibly different through this section, containing coarse, 'peaty' organic fragments.

Pollen and stomata

Thirty-three terrestrial pollen types, plus unknown and indeterminate (crumpled, degraded or obscured grains) were identified.

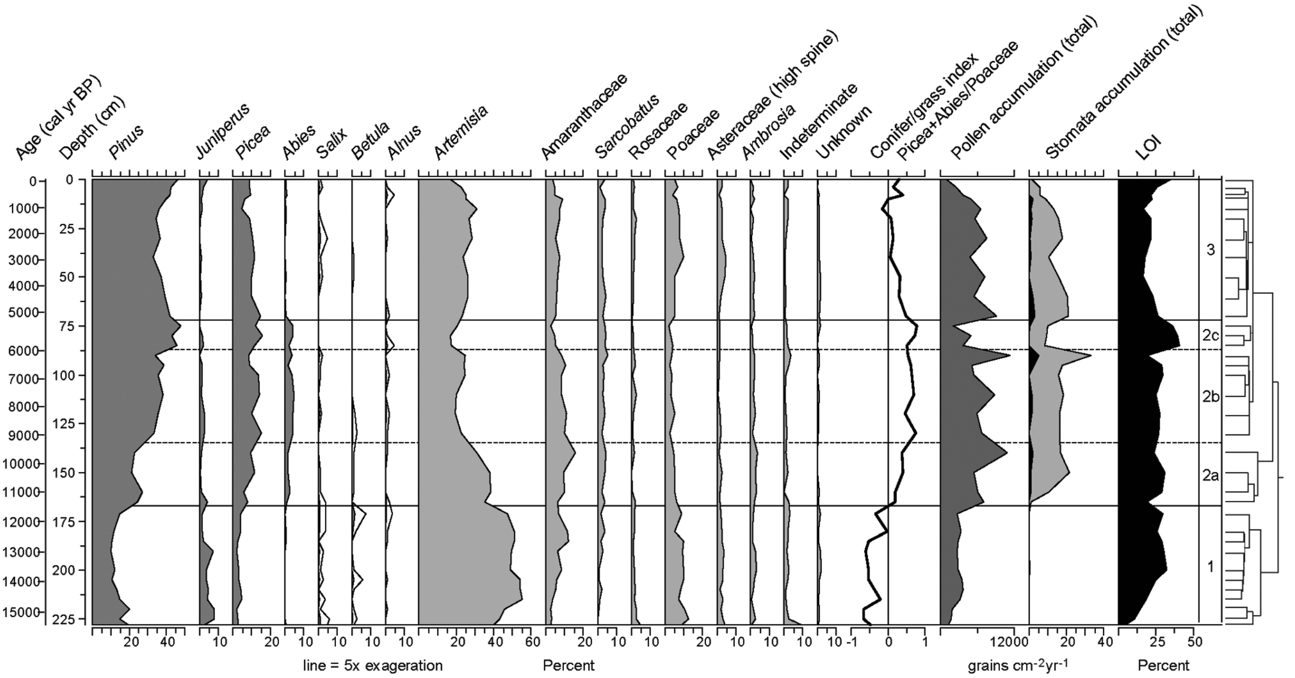

Figure 3. Percent pollen diagram of selected taxa and selected summary data. Shaded black portion of the stomata accumulation curve represents *Abies*. LOI: Loss on ignition. The conifer/grass index uses the formula $[(p+a)-po] / [(p+a)+po]$ where *p* is percent *Picea*, *a* is percent *Abies* and *po* is percent Poaceae. Values approaching 1 represent high levels of *Picea* and *Abies* presuming trees at or above modern treeline, while values approaching −1 represent abundant grass, expansion of tundra, and lower treeline

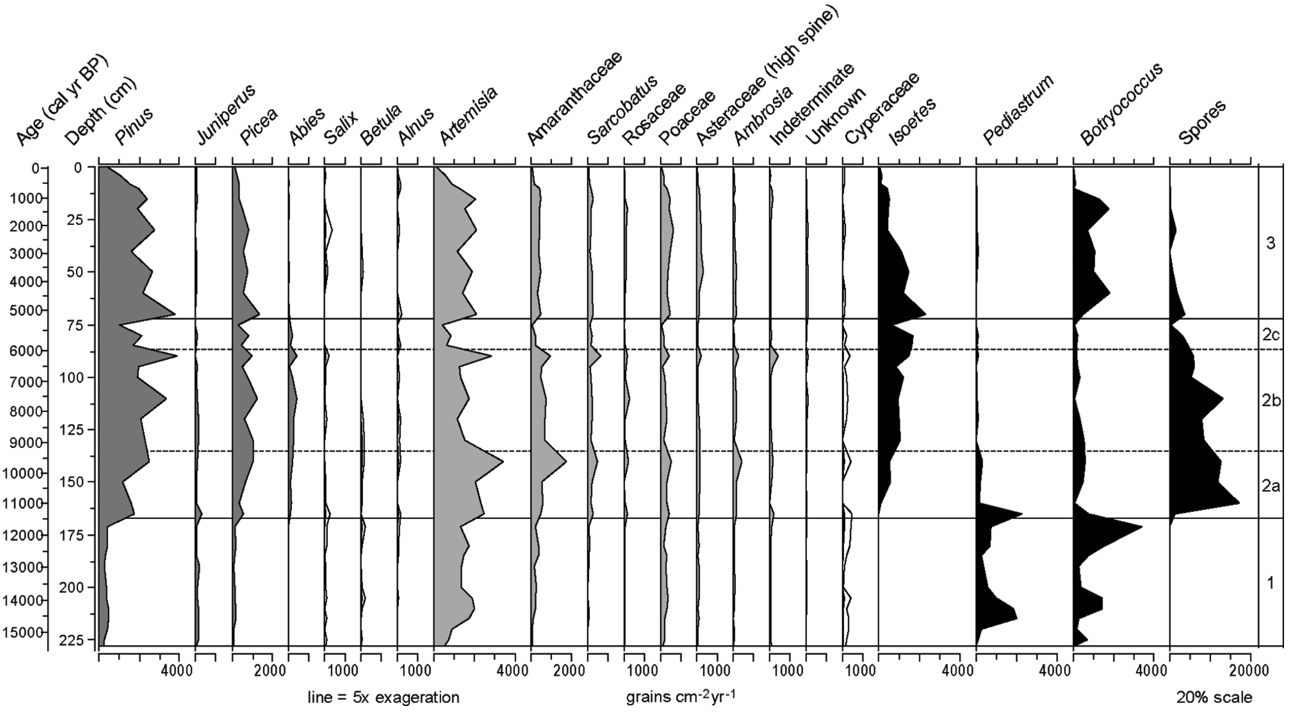

Figure 4. Accumulation rate diagram of selected terrestrial pollen, aquatic pollen, algae and spores

Pollen types with sums consistently >1% are presented here (Figure 3). We identified five aquatic pollen types (plants typically rooted in standing water such as Cyperaceae and *Isoetes*), two algae and several unidentified spores (Figure 4). Unknown spores were combined for graphic presentation since they all occurred in the same levels.

Zone 1 (15,330–11,500 cal. yr BP). Zone 1 (Figure 3) is dominated by high values of *Artemisia* (40–54%) and Poaceae (10–12%) and low values of *Pinus* (10–15%), *Picea* (2–4%), and *Abies* (0–1%). Conifer stomata are virtually absent. *Juniperus* values remain high (4–8%) between 15,330 and 13,000 cal. yr BP and then decline to ~2%. Rosaceae is present at very low levels throughout the core, but reaches its highest percentage (5%) in the basal sample. Pollen accumulation rates (Figure 4) support the pollen percentages throughout the core. Total pollen accumulation is low in Zone 1, averaging 3000 grains/cm^2 per yr. The highest accumulation rates are for *Artemisia* (~2000 grains/cm^2 per yr) and accumulation rates for Poaceae are greater than those for subalpine forest taxa such as *Picea* and *Abies* and nearly as high as those for *Pinus*. *Pediastrum* and *Botryococcus* are virtually absent from the basal sample, but increase rapidly upcore, after 15,000 cal. yr BP.

Zone 2 (11,500–5200 cal. yr BP). Zone 2a (11,500–9300 cal. yr BP) is transitional, characterized by decreasing abundance of *Artemisia*, *Juniperus*, and Poaceae, and increasing abundance of forest taxa, including *Picea*, *Abies* and *Pinus* (Figure 3). *Artemisia* decreases steadily from 47% to 22% while *Picea* increases from 4% to 10% and *Abies* from 1% to 4%. Conifer stomata (primarily *Picea* with small numbers of *Abies*) first appear at 11,300 cal. yr BP but increase rapidly, reaching their average abundance for the Holocene by 10,300 cal. yr BP. *Pinus* pollen doubles from 15% to 30%. Drought-tolerant shrubs and forbs, including Amaranthaceae and *Sarcobatus* also increase during this period.

Total pollen accumulation doubles in zone 2a, compared with zone 1. Although all taxa increase, rates of increase are greater for *Pinus*, *Picea* and *Abies* than for *Artemisia* and Poaceae, consistent with the percentage data. *Artemisia* remains the most abundant pollen type, but *Pinus* is nearly equal, having increased by nearly an order of magnitude. Similarly, there is a tenfold increase in the accumulation of *Picea* and *Abies* pollen as well as Amaranthaceae and *Sarcobatus*. *Pediastrum* and *Botryococcus* decline and are replaced by an unidentified spore (Figure 4). *Isoetes* first appears in abundance about 11,000 cal. yr BP.

In Zone 2b (9300–6000 cal. yr BP) *Artemisia* decreases, stabilizing at near modern percentages (~25%) and conifer pollen percentages remain high (*Pinus* ~36%, *Picea* ~12%, and *Abies* ~ 4%). Stomata accumulation remains constant except for a sharp increase at 6200 cal. yr BP, consistent with high pollen accumulation rates. Poaceae averages 4% and Amaranthaceae remains high at 10%. Total pollen accumulation is variable but remains high (between 5000 and 11,000 grains/cm^2 per yr). Spore accumulation slowly decreases as *Isoetes* increases in abundance.

Zone 2c (6000–5200 cal. yr BP) represents a short but distinct period of change. Organic content increases to its highest levels in the record, percentages of *Pinus*, *Picea*, and *Abies* all increase, and at the same time accumulation rates drop averaging 3600 grains/cm^2 per yr. *Pinus* and *Abies* accumulation rates decline slightly, but *Artemisia* pollen productivity falls to values below those in the Pleistocene. Conifer stomata accumulation rates also decline somewhat. Among aquatic taxa, *Isoetes* initially increases in abundance, then decreases abruptly; spores decline and no changes are seen in *Pediastrum*, *Botryococcus* or Cyperaceae.

Zone 3 (5200 cal. yr BP to present). Zone 3 is characterized first by an increase in shrubs and herbs, notably *Artemisia*, Amaranthaceae, Poaceae and Asteraceae, then a decline of these taxa towards the present. *Abies* all but disappears from the record while *Picea* remains relatively unchanged and *Pinus* increases. Conifer stomata accumulation is high initially, declines after ~4400 cal. yr BP, is variable until about 2000 cal. yr BP and then declines to the present. Pollen accumulation rates follow a similar pattern; initially high rates, 9000 grains/cm^2 per yr, followed by fluctuations around an average of 6000 grains/cm^2 per yr, and then a decline to 1000 grains/cm2 per yr after 1000 cal. yr BP. *Isoetes* remains high until about 3000 cal. yr BP, after which it declines to a minimum in the surface sediments. *Botryococcus* reappears in Zone 3 although it is largely absent in the surface samples, but *Pediastrum* does not return. Percent organic matter increases towards the top of the core to 35% in the surface sample.

Discussion

Vegetation reconstruction and comparison with regional records

Late Pleistocene 15,330 to 11,500 cal. yr BP. During the late Pleistocene, following glacial retreat ~15,330 cal. yr BP the local vegetation was characterized as alpine tundra, dominated by grasses (Poaceae), herbs (Asteraceae and Rosaceae) and scattered low growing willow (*Salix*) and birch (*Betula*), as well as sagebrush steppe (*Artemisia*) (Figure 3). Juniper, probably *J. communis* a prostrate shrub typical of high elevation environments, was also present and was probably the only conifer near the lake throughout the Late Pleistocene. *Picea*, *Abies* and *Pinus* (most likely *Pinus contorta*, the common *Pinus* species in the Snowy Range) were probably initially far downslope from the site, and migrated upwards with increased warming, nearing the site by the beginning of the Holocene ~11,500 cal. yr BP.

This picture of Late Pleistocene expansion of forests into high-elevation alpine-tundra and sagebrush-steppe is consistent with similar studies in the Rocky Mountains (Figure 5). High-elevation sites show a dominance of alpine-tundra and sagebrush-steppe in the Late Pleistocene (Fall, 1997; Fall et al., 1995; Vierling, 1998; Whitlock, 1993) with forests as much as 300–700 m downslope from their modern position (Fall, 1997). *Picea*, *Pinus* and *Abies* persisted in unglaciated habitats providing evidence that conifers were not displaced through glacial cycles (Whitlock, 1993). In Yellowstone National Park *Picea* was present at low elevation (2070 m) at 18,050 cal. yr BP and *Picea* parkland developed from ~ 13,380 to 12,350 cal. yr BP. Subalpine forests expanded and migrated upslope after about 13,380 cal. yr BP (Whitlock, 1993). In the Wind River Range conifers reached Rapid Lake (3134 m) by 13,150 cal. yr BP (Fall et al., 1995). In the southern Rocky Mountains, subalpine forest expanded rapidly upslope after 12,880 cal. yr BP with upper tree limit in central Colorado near 3250 m elevation (Fall, 1997). A subalpine forest dominated by *Picea, Abies* and *Pinus albicaulis* similar to today began to form about 12,350 cal. yr BP and by 11,620 cal. yr BP had extended into much of its modern range across the region (Fall, 1997).

Early and middle Holocene, 11,500–5200 cal. yr BP. The early and middle Holocene in the Rocky Mountains has been characterized by expansion of subalpine forests above modern treeline limits (Figure 5). Evidence that subalpine conifers reached the shore of EGL by 11,500 cal. yr BP comes from the first appearance of conifer stomata (Figure 3). The steady increase in conifer stomata, conifer pollen accumulation rate and percentage of *Picea* and *Abies* pollen between 11,500 and 9000 cal. yr BP suggests that a closed subalpine forest established around the lake (Figures 3 and 4). Closed spruce-fir forest is found ~40 m below the lake today, and we infer that treeline was at least 40 m higher at 9000

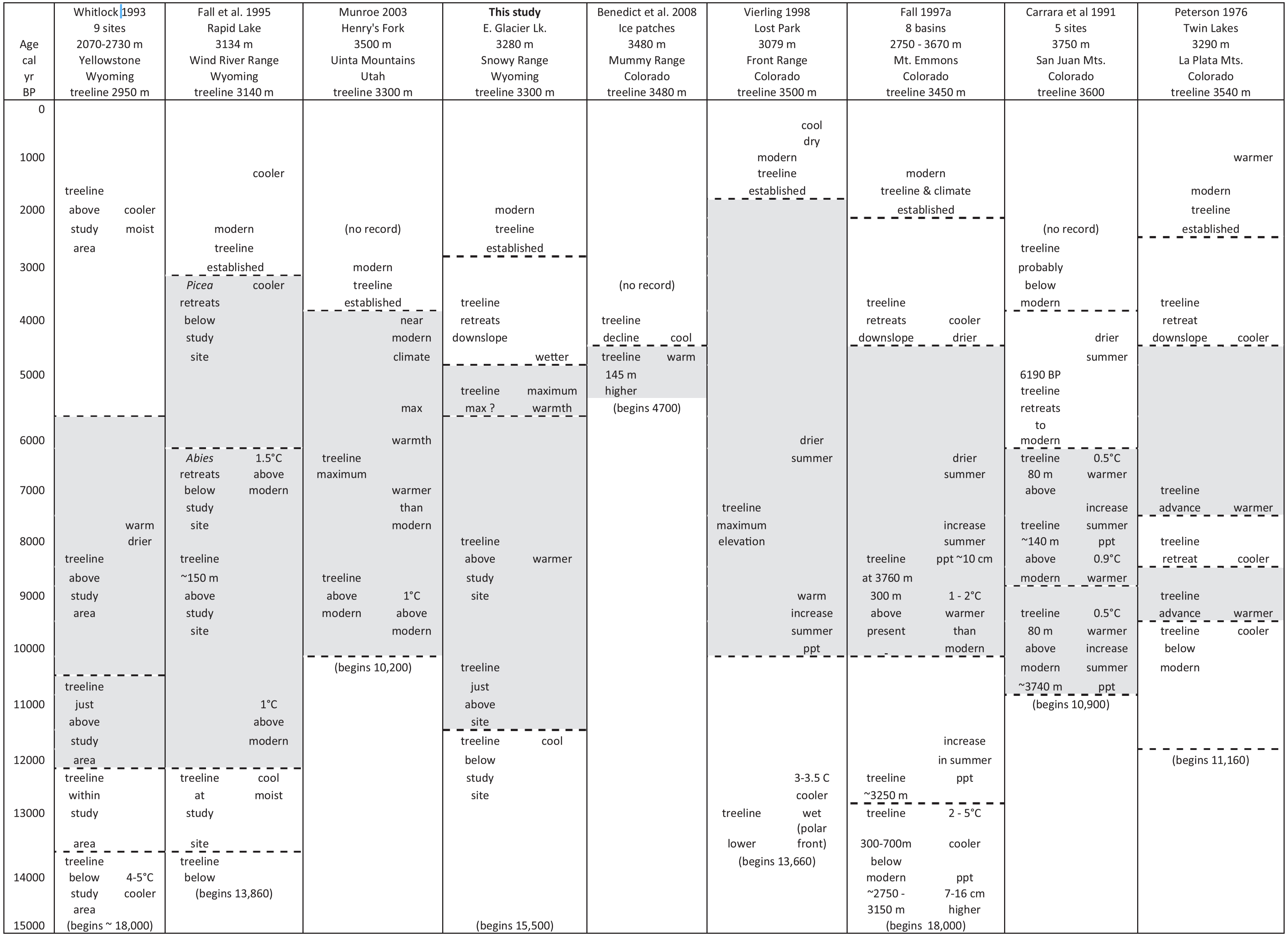

Figure 5. Vegetation and climate history from selected studies near upper treeline in the Rocky Mountains along a north to south transect. Dashed lines represent approximate timing of environmental changes identified in each record. Gray shading is periods of inferred higher treeline. All sites are shown in Figure 1

cal. yr BP. The conifer/grass index also suggests that alpine-tundra vegetation was displaced locally by subalpine forest.

Artemisia pollen accumulation rate increased between 11,500 and 9000 cal. yr BP even though percent *Artemisia* pollen declined (Figures 3 and 4). Percent *Pinus* pollen and accumulation rate both increased during this transitional period. These two genera are by far the largest pollen producers of all taxa in the record and one explanation for the sharp increase in accumulation rates after 11,500 is simply increased productivity with the onset of warmer Holocene temperatures. Another explanation is upward expansion of lodgepole pine parkland (*P. contorta*). Whitlock (1993) found a sharp increase in *P. contorta* pollen by 10,900 cal. yr BP at all sites in Yellowstone and argued that this represented the establishment of lodgepole pine forests. In the Snowy Range, lodgepole pine is not a common treeline species but is dominant below 3000 m, often forming dense forests (Dillon et al., 2005). Pines are highly productive long-distance pollen dispersers, and *Pinus* makes up >40% of the modern pollen in EGL (Figure 3). Given the small number of pines around the lake today (predominantly *P. flexilis*), it seems reasonable to conclude that pine pollen largely represents upslope transport from lower elevation lodgepole pine forests. We argue that the increase in pine pollen between 11,500 and 9000 cal. yr BP represents an initial expansion of lodgepole pine in the mixed conifer forests downslope from EGL (Minckley et al., 2012). Abundant *Artemisia* pollen suggests open 'parklands', but the steady increase in conifer pollen suggests a continued upward forest migration similar to what has been described by Fall et al. (Fall, 1997; Fall et al., 1995) in Wyoming and Colorado (Figure 5).

Between 9000 and 6000 cal. yr BP, studies throughout the region infer higher treeline (Figure 5). Maximum treeline advance ranged from 140 m in the San Juan Mountains (Carrara et al., 1991) and 150 m in the Wind River Range (Fall et al., 1995) to 300 m at Mount Emmons, Colorado (Fall, 1997). As expected given the complex topographic relief and latitudinal range of the studies, the exact timing and variation of treeline advance varies, however the overall picture is one of consistently higher treeline across the region during this time period.

Beginning about 6000 cal. yr BP there is evidence of forest change; however the pattern varies across the region. In Yellowstone, treeline retreated downslope and modern forest structure and limits appear to have been established ~5750 cal. yr BP (Whitlock, 1993). In the Wind River Range *Abies* moved downslope ~5990 cal. yr BP, but *Picea* remained above modern limits until 3160 cal. yr BP apparently reaching 150 m above modern sometime prior to 4200 cal. yr BP (Fall et al., 1995). Data from the Uinta Range (Munroe, 2003) are at low resolution (1 sample per 300–400 years) making it difficult to identify trends, however the *Picea/Pinus* ratio, used as a proxy for treeline change, suggest possible downslope movement of treeline between 5800 and 5500 cal. yr BP.

At EGL, there is clear evidence for environmental change at 6000 cal. yr BP. LOI values increase, *Isoetes* increases and sediments become peat-like, suggesting the presence of a more productive and possibly shallower lake. But the pollen data from EGL do not lead to a single clear interpretation of forest response during this time period. There is a decrease in conifer stomata and pollen accumulation rates but an increase in conifer pollen percentages. Lower stomata and pollen accumulation rates could be interpreted as a decrease in forest density and/or lower treeline. Stomata have been demonstrated to be indicators of the local presence of conifers, since they are remnant from needles that enter a lake (Hansen, 1995). An alternative hypothesis is that higher conifer pollen percentages represent an increase in forest density and/or treeline advance. The conifer/grass index argues for continued expansion of forest into the alpine-tundra zone. Calculation of accumulation rate is sensitive to changes in sedimentation rate and low stomata and pollen accumulation rates could be an artifact of high sedimentation rates during this period. The pattern of enhanced *Picea* and *Abies* percentages above treeline has been observed in modern pollen studies in western North America (Minckley and Whitlock, 2000; Minckley et al., 2008). The direction and magnitude of potential treeline movement at this time requires more detailed analysis to confidently resolve this question as the climatic tolerance of *Picea* and *Abies* overlap in temperature at the drier end of the moisture index (Minckley et al., 2008).

Sites in the southern Rocky Mountains of Colorado record varying evidence. In the San Juan Mountains, radiocarbon dating of buried *Picea* and *Abies* wood fragments demonstrated that treeline retreated 50 m downslope after 6190 cal. yr BP (Carrara et al., 1991). Further south in the Sangre de Cristo Mountains of northern New Mexico, maximum subalpine tree pollen at 5600 cal. yr BP suggests the highest treeline during the Holocene (Jiménez-Moreno et al., 2008). Other sites also record high treeline at 6000 cal. yr BP (Figure 5). At Mount Emmons (Fall, 1997) and the La Plata Mountains (Peterson and Mehringer, 1976), treeline does not retreat downslope until ~4500 cal. yr BP. No change is identified along the Colorado Front Range (Vierling, 1998) but this study is located well below treeline and has low sample resolution during this time period.

Late Holocene, 5200 cal. yr BP to the present. After 5200 cal. yr BP *Abies* was no longer an important component at EGL (Figure 3). Although conifer stomata and pollen accumulation rates again increase initially and treeline may have remained above modern elevation limits, after 4500 cal. yr BP there is consistent evidence for a more open forest. Engelmann spruce persisted as the dominant subalpine species, subalpine fir moved downslope, and we infer development of open parkland with expansion of alpine tundra. Modern treeline appears to have become established about 3000 cal. yr BP, although the forest may have begun to expand again in the last few centuries.

The EGL record has several features similar to the Wind River Range in west central Wyoming. There, *Abies* moved downslope after 5990 cal. yr BP, but *Picea* remained 150 m above modern limits until sometime before 4200 cal. yr BP, then treeline retreated downslope, reaching modern limits at 3160 cal. yr BP (Fall et al., 1995). Downslope movement of upper treeline after ~4500 cal. yr BP is a fairly consistent pattern throughout the Rocky Mountains with establishment of modern treeline between about 3000 and 2000 years ago. In the Mummy Range of northern Colorado, Engelmann spruce growing at treeline (3480 m) have establishment dates between 4700 and 4470 cal. yr BP and death dates of 4200 cal. yr BP (Benedict et al., 2008). Ice and snow permanently buried these trees, helping preserve them intact until modern time. Sites in the southern Rocky Mountains nearly all record downslope retreat of treeline after 4500 cal. yr BP reaching modern limits between 2500 and 2000 cal. yr BP (Figure 5).

Paleoclimate interpretation

Late Pleistocene 15,500 to 11,500 cal. yr BP. Our record of expanded alpine tundra in the Late Pleistocene supports an interpretation of colder temperatures until at least 11,500 cal. yr BP when expansion of forests indicates increasingly warmer temperatures. Late Pleistocene temperature reconstructions in the Northern and Southern Rocky Mountains appear regionally synchronous during this period (Figure 5), with estimates of temperatures between 2° and 5°C cooler than modern (Fall, 1997; Maher, 1972; Vierling, 1998; Whitlock, 1993).

Early and middle Holocene, 11,500–5200 cal. yr BP. Though there is regional variation, sites in the Northern and Southern Rocky Mountains record higher temperatures and treeline at or above modern elevations by 10,000 cal. yr BP (Figure 5). Reconstructed temperatures range from 0.5° to 2°C above modern. Estimates for the timing of maximum warmth vary considerably between sites, but all sites indicate warmer climate lasting until at least 6000 cal. yr BP, consistent with maxima in solar forcing. Whitlock and Bartlein (1993) argued that early-Holocene warmth would increase aridity through higher evapotranspiration rates at sites under the subtropical high, but increase precipitation at sites affected by the summer monsoon. Colorado is more strongly affected by summer monsoon precipitation than Wyoming (Shinker, 2010), and the paleoecologic studies from these different regions reflect this difference. In Yellowstone, Whitlock (1993) describes expansion of Douglas-fir forest (*Pseudotsuga menzeseii*) as evidence for increased summer drought. Fall et al. (1995) argue that warm dry conditions at low elevation forced forests to migrate upslope. The same conditions existed in the Snowy Range. We interpret the upward shift in treeline as a result of warmer than modern temperatures and increased aridity at lower elevations. Studies from southern Colorado describe increased summer precipitation in the early Holocene, leading to increasingly drier summers by 6000 to 5000 cal. yr BP (Carrara et al., 1991; Fall, 1997; Vierling, 1998).

The environment changed for about an 800 year period between 6000 and 5200 cal. yr BP. We present several climatic and environmental hypotheses to explain this interval. The first hypothesis suggests a period of intensified warmth and aridity and increased forest density and/or upslope migration. The bathymetry of EGL reveals a large shelf (Figure 1) so that a 2 m drop in surface elevation would result in substantial reduction of surface area and water volume and potentially eutrophication. A smaller, warmer lake surrounded by subalpine forest would enhance *Isoetes* productivity and organic matter (Vöge, 2006), create a smaller more enclosed lake that received less pollen from distant sources (particularly *Pinus* and *Artemisia*, the two dominant regional pollen producers), and increase the percent of local pollen types, such as *Picea* and *Abies*. Under sufficiently warm conditions, lodgepole pine may have migrated close enough to the lake to increase the percent pollen contribution, however long-distance transport is more likely. This explanation does not account for the decline in conifer stomata accumulation rates, which would be expected to increase with more trees near the lake shore, unless the apparent decrease is simply an artifact of higher sedimentation rates. Alternatively, a lower lake would result in a greater littoral zone filtering terrestrial inputs into the depocenter of the lake. The hypothesis of warmer summer temperatures is consistent with the two nearest equivalent study sites; one in the Wind River Range, Wyoming (280 km northwest) (Fall et al., 1995; Brunelle and Minckley, unpublished data, 2010) and the other in the Mummy Range of northern Colorado (100 km southeast) (Benedict et al., 2008) (Figure 1). About 6160 cal. yr BP, subalpine fir migrated downslope in the Wind River Range but Engelmann spruce remained at high elevation. Fall et al. (1995) argued that fir could not tolerate high summer temperatures and required deeper snowpack than spruce. They suggested increased aridity and decreased summer snowpack associated with summer temperatures 1.5°C higher than modern. Treeline remained high until about 4200 cal. yr BP, then retreated downslope. In the Mummy Range, spruce grew above modern timberline at least as early as 4700 cal. yr BP, providing evidence of warmer summer temperatures (Benedict et al., 2008).

There is also the possibility that it was warmer and wetter. Little Windy Hill Pond in the Medicine Bow Mountains has evidence that lake levels began to increase sometime between 5600 and 5200 cal. yr BP (Minckley et al., 2012). Under this hypothesis, increased precipitation would support increased forest cover (higher percentages conifers) and a decrease in parkland taxa (lower percentages of shrubs and grasses). However, conifer pollen accumulation rates decline somewhat during this period, and under conditions of a closed forest pollen production and conifer stomata accumulation would have been expected to increase.

A third hypothesis suggests increased aridity and cooler summer temperatures. Under this interpretation, reduced stomata accumulation suggests fewer trees associated with a shorter growing season that precluded tree establishment (Moir et al., 1999). This explanation is consistent with the rapid decline in treeline in the San Juan Mountains associated with cooling of 0.5°–0.9°C (Carrara et al., 1991); however this hypothesis does not explain the high accumulation rate of organic material and also assumes a local climatic response similar to a more distant site (430 km south). A final hypothesis is the removal of trees by a catastrophic fire. Forest re-establishment on burned sites at or above treeline is problematic and may take up to 1000 years for regrowth (Billings, 1969; Maher and Germino, 2006). We found no significant charcoal layer to support this hypothesis. Further, charcoal analysis from Little Brooklyn Lake fails to identify any significant fires in the Snowy Range about this time (Brunelle and Minckley, unpublished data, 2010).

We argue that the first hypothesis, maximum upper treeline extent during a period of warmer drier climate, best explains the evidence. This conclusion is supported by other regional studies, however as noted earlier, there is considerable variation, potentially associated with local conditions created by the complex topography (Figure 5). Low lake levels are evident through much of the Rocky Mountains during this time (Shinker et al. 2010; Shuman et al., 2009, 2010). The first record of establishment of *J. osteosperma*, a drought-tolerant species, at the lower treeline (1300–1400 m) in the Bighorn Basin of Southern Montana about 5400 cal. yr BP supports an interpretation of dry climate (Lyford et al., 2002). But the regional picture remains complicated. The nearby Little Windy Hill Pond site has lake levels ~1 m below modern from 7000 cal. yr BP until sometime between 5600 and 5200 cal. yr BP, which is consistent with other records except that the timing of the termination of the drought and initiation of wetter climate remains unclear. Analysis of artiodactyl populations in the Wyoming Basin showed increases in populations of grazers, associated with cooler but wetter climate sometime between 6800 and 5800 cal. yr BP (Byers and Smith, 2007), further indicating that more work is needed to explain the climate during this period.

Late Holocene, 5200 cal. yr BP to the present. Cooler wetter conditions appear to have returned about 5200 cal. yr BP. By about 4500 cal. yr BP cooler climate is recorded across the region, with lower treeline (Figure 5). Modern climate and treeline appear to have been established at most sites by ~3000 cal. yr BP.

Conclusions

Deglaciation at EGL occurred by ~15,330 cal. yr BP although temperatures were probably still ~2° to 5°C colder than modern at that time and treeline was downslope. Treeline reached the lake by the beginning of the Holocene ~11,500 cal. yr BP and continued migrating upslope to about 40 m higher than modern by 9000 cal. yr BP in association with warm dry climate. Peaty sediments between 6000 and 5200 cal. yr BP indicate a more productive and possibly shallower lake during an extended dry period. The pollen and stomata evidence during this period could be interpreted as either higher treeline with increased forest density, or lower treeline with a decrease in forest density. We argue that treeline remained high and that temperatures may have increased during this period. After 5200 cal. yr BP *Abies* retreated below the elevation of EGL and modern treeline became established ~3000 cal. yr BP. There is increasing evidence for persistent drought between 6000 and 5200 cal. yr BP, although the complex topography within the Rocky Mountains makes it challenging to identify broad regional patterns over short time periods. Gaining a better understanding of the magnitude and extent of climate change has become increasingly important given climate model predictions for future climate. This is particularly important at high elevations where changes are predicted to be more severe. Further studies of sites along high elevation gradients like the Glacier Lakes Basin are warranted to help reconstruct the complex response to Holocene climate change.

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