Quaternary Research 82 (2014) 618–634

Contents lists available at ScienceDirect

Quaternary Research

journal homepage: www.elsevier.com/locate/yqres

Summary of the Snowmastodon Project Special Volume

A high-elevation, multi-proxy biotic and environmental record of MIS 6–4 from the Ziegler Reservoir fossil site, Snowmass Village, Colorado, USA

Ian M. Miller [a,*], Jeffrey S. Pigati [b], R. Scott Anderson [c], Kirk R. Johnson [a,d], Shannon A. Mahan [e], Thomas A. Ager [b], Richard G. Baker [f], Maarten Blaauw [g], Jordon Bright [h], Peter M. Brown [i], Bruce Bryant [b], Zachary T. Calamari [j,l], Paul E. Carrara [b], Michael D. Cherney [j,l], John R. Demboski [a], Scott A. Elias [k], Daniel C. Fisher [j,l], Harrison J. Gray [e], Danielle R. Haskett [m], Jeffrey S. Honke [b], Stephen T. Jackson [n,o], Gonzalo Jiménez-Moreno [p], Douglas Kline [a], Eric M. Leonard [q], Nathaniel A. Lifton [r], Carol Lucking [a], H. Gregory McDonald [s], Dane M. Miller [n], Daniel R. Muhs [b], Stephen E. Nash [a], Cody Newton [t], James B. Paces [u], Lesley Petrie [v], Mitchell A. Plummer [w], David F. Porinchu [m], Adam N. Rountrey [l,x], Eric Scott [y], Joseph J.W. Sertich [a], Saxon E. Sharpe [z], Gary L. Skipp [b], Laura E. Strickland [b], Richard K. Stucky [a], Robert S. Thompson [b], Jim Wilson [aa]

[a] *Denver Museum of Nature and Science, 2001 Colorado Boulevard, Denver, CO 80205, USA*
[b] *U.S. Geological Survey, Denver Federal Center, Box 25046, MS-980, Denver, CO 80225, USA*
[c] *School of Earth Sciences and Environmental Sustainability, Northern Arizona University, Flagstaff, AZ 86011, USA*
[d] *National Museum of Natural History, Smithsonian Institution, Box 37012, MRC 106, Washington, DC 20013, USA*
[e] *U.S. Geological Survey, Denver Federal Center, Box 25046, MS-974, Denver, CO 80225, USA*
[f] *Department of Earth and Environmental Sciences, University of Iowa, Iowa City, IA 52242, USA*
[g] *School of Geography, Archaeology and Palaeoecology, Queen's University Belfast, BT7 1NN Belfast, UK*
[h] *Department of Geosciences, University of Arizona, Tucson, AZ 85721, USA*
[i] *Rocky Mountain Tree-Ring Research, 2901 Moore Lane, Fort Collins, CO 80526, USA*
[j] *Department of Earth and Environmental Sciences, University of Michigan, 1100 North University Avenue, Ann Arbor, MI 48109, USA*
[k] *Geography Department, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK*
[l] *University of Michigan Museum of Paleontology, 1109 Geddes Avenue, Ann Arbor, MI 48109, USA*
[m] *Department of Geography, University of Georgia, Athens, GA 30602, USA*
[n] *Department of Botany, University of Wyoming, Laramie, WY 82071, USA*
[o] *Southwest Climate Science Center, Institute of the Environment, University of Arizona, 715N. Park Ave., Tucson, AZ 85719, USA*
[p] *Departamento de Estratigrafía y Paleontología, Universidad de Granada, Fuente Nueva s/n, 18002 Granada, Spain*
[q] *Department of Geology, Colorado College, Colorado Springs, CO 80903, USA*
[r] *Department of Earth, Atmospheric, and Planetary Sciences, and Physics and Astronomy, Purdue University, West Lafayette, IN 47907, USA*
[s] *Museum Management Program, National Park Service, 1201 Oakridge Drive, Fort Collins, CO 80525, USA*
[t] *Department of Anthropology, University of Colorado, Boulder, CO 80309, USA*
[u] *U.S. Geological Survey, Denver Federal Center, Box 25046, MS-963, Denver, CO 80225, USA*
[v] *Department of Earth and Planetary Sciences, University of California Santa Cruz, Santa Cruz, CA 95064, USA*
[w] *Idaho National Laboratory, P.O. Box 1625, Idaho Falls, ID 83415, USA*
[x] *Centre for Marine Futures, Oceans Institute, University of Western Australia, M470 35 Stirling Highway, Crawley, WA 6009, Australia*
[y] *San Bernardino County Museum, 2024 Orange Tree Lane, Redlands, CA 92374, USA*
[z] *Desert Research Institute, 2215 Raggio Parkway, Reno, NV 89512, USA*
[aa] *Aeon Laboratories, LLC, 5835 N Genematas Drive, Tucson, AZ 85704, USA*

ARTICLE INFO

Article history:
Received 3 May 2014
Available online 25 October 2014

Keywords:
Rocky Mountains
Sangamon interglacial

ABSTRACT

In North America, terrestrial records of biodiversity and climate change that span Marine Oxygen Isotope Stage (MIS) 5 are rare. Where found, they provide insight into how the coupling of the ocean–atmosphere system is manifested in biotic and environmental records and how the biosphere responds to climate change. In 2010–2011, construction at Ziegler Reservoir near Snowmass Village, Colorado (USA) revealed a nearly continuous, lacustrine/wetland sedimentary sequence that preserved evidence of past plant communities between ~140 and 55 ka, including all of MIS 5. At an elevation of 2705 m, the Ziegler Reservoir fossil site also contained

---

* Corresponding author.
E-mail address: ian.miller@dmns.org (I.M. Miller).

http://dx.doi.org/10.1016/j.yqres.2014.07.004

Keywords (cont'd):
Paleoclimate
Ziegler Reservoir
Marine Oxygen Isotope Stage
Mammut americanum
Mammuthus columbi

thousands of well-preserved bones of late Pleistocene megafauna, including mastodons, mammoths, ground sloths, horses, camels, deer, bison, black bear, coyotes, and bighorn sheep. In addition, the site contained more than 26,000 bones from at least 30 species of small animals including salamanders, otters, muskrats, minks, rabbits, beavers, frogs, lizards, snakes, fish, and birds. The combination of macro- and micro-vertebrates, invertebrates, terrestrial and aquatic plant macrofossils, a detailed pollen record, and a robust, directly dated stratigraphic framework shows that high-elevation ecosystems in the Rocky Mountains of Colorado are climatically sensitive and varied dramatically throughout MIS 5.

Introduction

Floral and faunal communities dating to Pleistocene interglacial periods offer opportunities to understand the structure and composition of modern ecosystems. They also offer a framework to evaluate the long-term dynamics of vertebrate and invertebrate faunas in different environments and habitats and to analyze the impact that millennial-scale climate change can have on various ecological systems. Marine Oxygen Isotope Stages (MIS) 31 (1.081–1.062 Ma) and 11 (424–374 ka) [MIS ages from Lisiecki and Raymo (2005)] are often cited as climatic analogs to the present day because their orbital parameters (eccentricity, obliquity, and axial precession) are similar to those of the Holocene (Loutre and Berger, 2003; EPICA community members, 2004; Scherer et al., 2008; Rohling et al., 2010; Tzedakis, 2010; Fawcett et al., 2011). However, direct comparison and evaluation of specific aspects of modern terrestrial ecosystems with either MIS 31 or 11 can be difficult for a number of reasons. First, the impact of geomorphic processes (erosion, burial, soil formation, diagenesis) increases with age, thus removing or altering the primary record at sites dating to either MIS 31 or 11 and resulting in a fragmented view of the reconstructed systems. Second, the introduction, evolution, and/or exodus of various biotic components within an area over long timescales can lead to fundamental reorganizations of population structures, including no-analog communities that hinder or complicate comparisons with modern environments (Williams et al., 2004; Williams and Jackson, 2007). Finally, even in the most ideal ecological and environmental settings, establishing robust chronologies for terrestrial deposits of such antiquity is challenging because the precision and accuracy of most chronometric techniques decreases substantially with age. Eventually, given enough time, the magnitude of the age uncertainties may exceed the duration of the period of interest, thus prohibiting clear, unambiguous correlation between chronometric ages and Marine Oxygen Isotope Stages.

MIS 5 (~130–74 ka), also called the Last Interglacial Period *sensu lato*, offers a reasonable alternative to MIS 31 and 11 for comparison with the Holocene, albeit with a few caveats. MIS 5 and the Holocene (or MIS 1) were (are) both subject to relatively high insolation values (Berger and Loutre, 1991; CAPE-Last Interglacial Project Members, 2006). However, the amplitude of insolation change at northern mid-latitudes (June/December at 30°N, for example) was larger during MIS 5 than it has been for the Holocene, which has significant implications for climate, vegetation, and faunas. Despite this difference, there are more known sites containing terrestrial proxy information that date to MIS 5 than to either MIS 31 or 11, and the MIS 5 sites are commonly better preserved than their older counterparts. Even with the increased number of sites and better preservation, however, the number of well-dated, last interglacial terrestrial records that include both floral and faunal components is still relatively small, especially in North America. Pollen records from deep-sea cores taken near the California/Oregon and South Carolina/Georgia coasts, for example, cover MIS 5 in some detail (Heusser, 2000; Lyle et al., 2001; Pisias et al., 2001; Heusser and Oppo, 2003), but they do not contain terrestrial vertebrate or invertebrate fossils. Similarly, terrestrial MIS 5 sites that contain abundant fossils often lack adequate chronologic control or have not been analyzed for the full suite of environmental proxies that may be available (Bell et al., 2004). Thus, our view of MIS 5 in North America, even under the best of circumstances, is fragmentary.

In the interior of North America, we have only a crude understanding of terrestrial biotic communities for the Last Interglacial Period (Pinsof, 1996). Our view is heavily biased by the fact that there are only a few sites at which some combination of insects, other invertebrates, micro- and macro-plants, and micro- and macro-vertebrate fossils have been preserved, collected, and studied in detail (see Muhs et al., 2001 for a review of records from Alaska; Graham and Lundelius, 2010). Moreover, only a small percentage of these sites combine robust chronologies and a comprehensive analysis of the local environmental context over a significant span of time (i.e., >10,000 yr) (Scott et al., 1982; Pinsof, 1997). Finally, only the American Falls (Pinsof, 1996), Bear Lake (Jiménez-Moreno et al., 2007; Kaufman et al., 2009) and Yellowstone (Baker, 1986) sites are situated above 1000 m (Fig. 1) and, of these, only American Falls contains vertebrate fossils, leaving alpine systems in the continental interior during MIS 5 sparsely documented.

In 2010–2011, construction to enlarge a reservoir near Snowmass Village, Colorado (USA) in the Rocky Mountains (Fig. 1) revealed Pleistocene lacustrine sediments that contained well-preserved plant, invertebrate, and vertebrate fossils (see the detailed studies in this volume for full presentations). An analysis of the geologic setting and stratigraphy (Pigati et al., 2014-in this volume), combined with direct dating of the lake sediment, fossils, and the impounding moraine using multiple chronometric methods (Mahan et al., 2014-in this volume), has revealed a nearly continuous, fossil-rich sedimentary sequence spanning ~140 to 55 ka, representing the end of MIS 6, all of MIS 5 and MIS 4, and the beginning of MIS 3. This site, termed the Ziegler Reservoir fossil site (ZRFS), contains long-term, multi-proxy records of biodiversity and climate change, including the most complete, high-elevation record of MIS 5 yet reported in North America.

This article is a synthesis of the data presented throughout this special volume of *Quaternary Research*, which represents the first comprehensive scientific report of the ZRFS. The primary goals of this paper are to (1) place the fossil animals and plants in an environmental context in order to reconstruct the ecosystems in which they lived; and (2) document the response of these local ecosystems to established global climate conditions during MIS 6/5/4 in order to gain insight into the response of ecosystems in the Rocky Mountains of Colorado to past and potentially future climate change.

Materials and methods

The “Snowmastodon Project,” as the investigations came to be known, was essentially a paleontological salvage effort of an active construction site (Fig. 2). As a result, most of the contextual data were destroyed as the project unfolded. Early on, it was obvious that we needed to define the site stratigraphy, establish a sample nomenclature system, and expose stratigraphic sections that could be sampled repeatedly over the duration of the project so that the invertebrate paleontological, paleoenvironmental, and geochemical proxy data could be compared within a common stratigraphic and chronologic framework.

In May 2011, scientists and volunteers from the Denver Museum of Nature and Science (DMNS) dug multiple trenches (including localities 49 and 51) and enhanced a 4-m-high, human-constructed outcrop (Locality 43) in the interior portion of the lake basin that exposed a majority of the lacustrine sedimentary sequence (Fig. 2). These exposures were complemented by a series of sediment cores taken from the lake

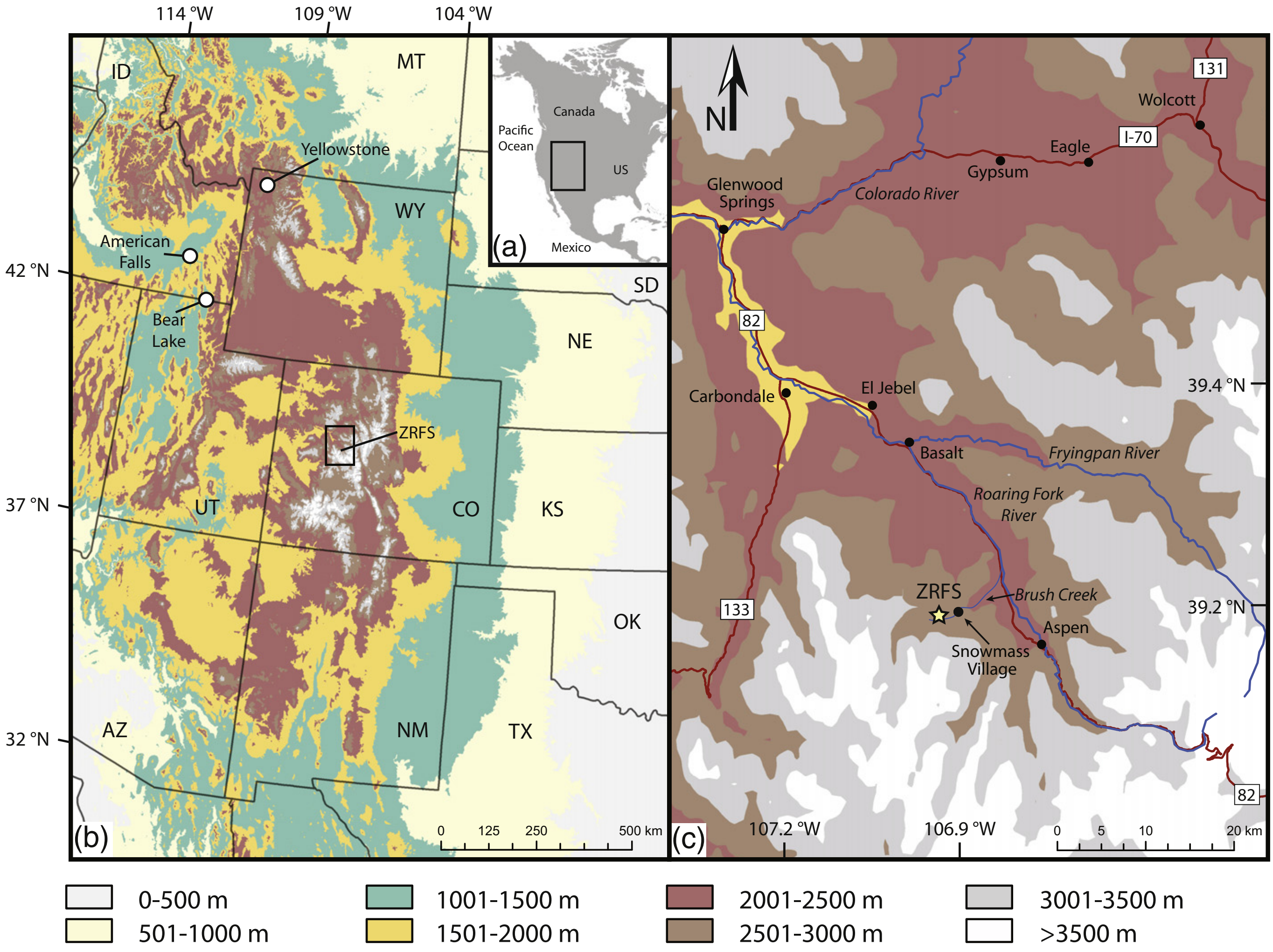

Figure 1. Site location maps for the Ziegler Reservoir fossil site (ZRFS). Inset box in (a) shows the area enlarged in (b). Maps (b, c) are color-coded by elevation to highlight that the ZRFS lies within one of the highest elevation regions of the Rocky Mountains. Map (b) also shows the locations of paleontological sites at American Falls, Yellowstone, and Bear Lake (circles), which are the only sites in North America other than the ZRFS (inset box) that contain a Marine Oxygen Isotope Stage (MIS) 5 record and are situated above 1000 m above sea level (see text for discussion). The inset box in (b) located in the middle of the state of Colorado shows the area enlarged in (c). The star in map (c) shows the location of the ZRFS at 39.2075°N and 106.9648°W at an elevation of 2705 m. Major rivers appear in blue and are labeled in italics. Brush Creek, which is adjacent to the ZRFS, is the only minor stream shown on the map (also in blue and labeled in italics). Major roads appear in red and are labeled with their highway designations. Black dots show the location of local municipalities.

interior, which provided an essentially continuous sequence of lake-center sediments and extended into lacustrine and glacial units not exposed in either the trenches or outcrop. Environmental proxy samples collected by the various scientists were taken at these trenches and outcrops, as well as from the cores.

The complex stratigraphy of the lake-margin sediments, which contained the majority of the large vertebrate fossils, was documented through the course of the excavation and was continually tied to the lake-center sediments using stratigraphy and precise elevation measurements. Elevations for all stratigraphic sections, numbered locality stakes, stratigraphic horizons, and discrete bone occurrences were established using a local datum and a Total Station (Topcon GTS-230 W gun)[1], providing an overall x–y–z control with a precision of ~10–30 cm (Fig. 3). In addition to the larger salvage operations, three partial mammoth skeletons outside the dam emplacement area between the eastern edge of the basin and Locality 43 were treated as archeological excavations as described by Fisher et al. (2014-in this volume). A complete account of the data collection and field methods is provided by Lucking et al. (2012).

Environmental proxy samples collected by the project scientists are housed at their respective institutions. Geologic samples and sediment cores are archived currently at the U.S. Geological Survey in Denver, Colorado. Faunal and floral remains collected by DMNS personnel are cataloged and archived in the Earth Sciences collections at the Museum.

Site description

A brief summary of the geologic setting and stratigraphy, as well as the chronology, is presented below. A detailed summary of these topics is provided in the Supplemental Information. Additional information can be found in Pigati et al. (2014-in this volume) and Mahan et al. (2014-in this volume).

Geologic setting and stratigraphy

During the latter part of the Bull Lake glaciation, ~155–130 ka (Licciardi and Pierce, 2008), Snowmass Creek Valley, which is located

---

[1] Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

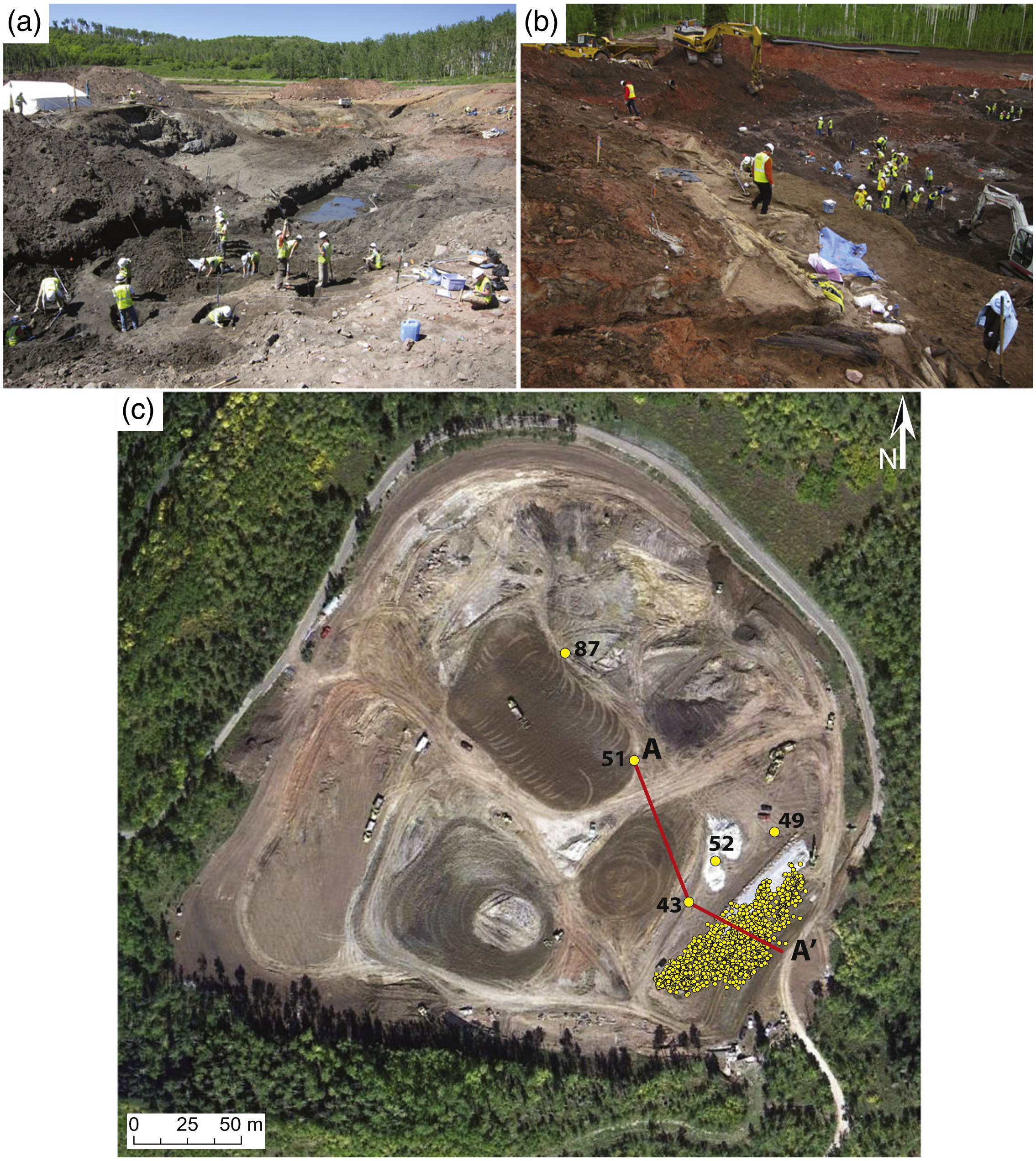

Figure 2. Site photographs taken in June (a, b) and August (c) of 2011 (photos courtesy of Rick Wicker, Denver Museum of Nature and Science). Photograph (a) is a view looking north from the southern end of the bone cloud (see photograph c). The large stepped wall of sediment on the left hand side of the frame immediately adjacent to the white tent is Locality 43. This locality represents the main lake-center sampling site. The far right corner of the photograph in panel (a) shows the area known as "the beach" (Brown et al., 2014-in this volume), which is the location from which the photograph in (b) was taken. Photograph (b) is a view looking south from the northern end of the bone cloud. Locality 43 is immediately out of the frame to the right. The foreground shows the oriented tree fossils that were preserved in the Beach Silt. The location of the large excavator shows the approximate location from which the photograph in (a) was taken. Aerial photograph (c) shows the location of the cross-section (red line, A to A′) from Pigati et al. (2014-in this volume) used in Fig. 4. The large, labeled yellow dots show the location of major localities discussed in the text and in Pigati et al. (2014-in this volume). The small yellow dots show the location of each of the more than 5000 large fossil bones collected at the site, collectively referred to as the "bone cloud" (also shown in Fig. 3). The disturbed surface in the photograph roughly corresponds to the extent of the paleo-lake.

immediately west of the ZRFS (Fig. 1C), hosted a large glacier that extended nearly 26 km downslope, was more than 250 m thick, and terminated ~8 km downvalley of the fossil site at an elevation of 2315 m. At the glacial maximum, when temperatures were ~5–9 °C colder than today (Leonard et al., 2014-in this volume), the glacier was thick enough to overtop the eastern wall of the valley and spill into the head of the Brush Creek drainage system (Fig. 1C). As the Brush Creek lobe receded, it left behind a small moraine that impounded a ~14.2 ha drainage basin, forming a small alpine or subalpine lake that was initially ~10 m deep. Over time, the lake filled with sediment, transforming first into a marsh or wetland, and later into an alpine meadow. When glacial conditions returned to the Rocky Mountains during Pinedale time (MIS 2), conditions were not as cool and (or) wet as during the Bull Lake glaciation. Thus, the Pinedale glacier that flowed down Snowmass Creek Valley was not quite thick enough to overtop the valley wall near the ZRFS and the lake sediments and fossils deposited there previously were left untouched.

When scientists arrived in October 2010, much of the sediment in the southeast quadrant of the site had been removed as part of the reservoir enlargement project (Fig. 2a, b; Fig. 4a). Sediments in the interior part of the basin were generally well sorted and fine grained (silt/clay). Discrete units could be traced laterally across the site. A total of 18 units

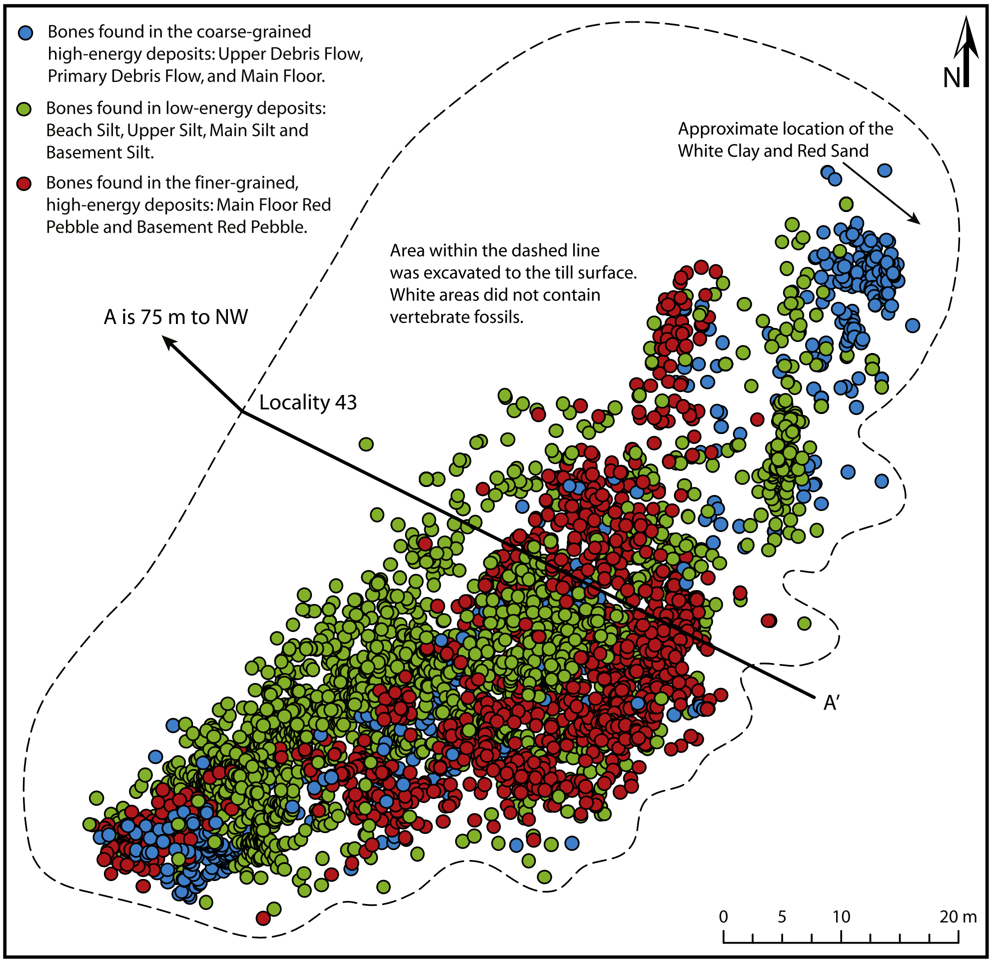

Figure 3. Map showing an expanded view of the "bone cloud," which shows the locations of the more than 5000 large fossil bones that were recovered at the site. Each colored point is the mapped location of a large fossil bone. The colors correspond to the broad depositional category of the sediments in which they were found. The units are listed by their field names [see Pigati et al. (2014-in this volume) for descriptions of these units]. An additional 26,000+ small bones have been recovered since the excavation through sieving, nearly all belonging to *Ambystoma tigrinum* (tiger salamander). The location of cross-section A–A′ (Fig. 4) is shown by the thick black line. The dashed line shows the approximate extent of the area that was excavated to the till surface. Additional large areas of the paleo-lake to the northwest of this map were excavated but only to shallow depths (2–3 m).

were identified in the interior portion of the lake based on field texture, bedding, and color, including 16 fine-grained units that together are ~10 m thick, glacial till (Unit 2), and the underlying Mancos Shale (Unit 1, which was observed outside the excavation pit nearby). Thicknesses of the fine-grained sediments range from ~12 cm (Unit 12) to ~1.5 m (Unit 18), with clear to abrupt contacts between each unit. The amount of organic material present in each unit is highly variable, ranging from negligible (units 13 and 14) to common (most units) to extremely abundant (units 12 and 15). The sediments are composed predominantly of silt, which accounts for 40–80% of the total volume, reaching maximum concentrations in units 10–14. Clay content ranges from 10 to 40% and is highest near the base (units 3–4) and top of the profile (units 15–18). Silicates dominate the mineralogy of the lake-center sediments, as the very-fine-sand fraction is composed of quartz (78–90%), feldspar (6–19%), and mica (<5%). Similar ranges are observed for the silt-size fraction, with the addition of chlorite in concentrations ranging up to ~2%.

In contrast to the sediments present in the middle of the basin, the lake-margin sediments are composed of a complex sequence of colluvial diamictite units interfingered with fine-grained lacustrine sediments, some of which are correlative to the lake-center sediments (Fig. 4a). The stratigraphy of the lake-margin sediments represents an infilling sequence recording predominantly near-shore, subaqueous deposition, punctuated by brief intervals of subaerial exposure (as indicated by fossils and iron oxidation states) and moraine slope failures. The coarse-grained diamictite units are poorly sorted, contain clasts up to 1 m or more in diameter, and typically extend ~50 m from the inner slopes of the moraine toward the basin center before pinching out. Along the strike of the lake-margin sediments, there are marked changes in bed thickness, grain-size, sorting, and dip within each unit. Additionally, contacts between the units often exhibit considerable topography. With few exceptions, the fine-grained sediments that are interbedded with the diamictites are well sorted and massive, and appear to grade into the lake-center sediments.

We identified three marker beds within the stratigraphic section that were used to correlate lake-center sediments, where most of the chronologic and paleoenvironmental proxy sampling took place, and the lake-margin sediments, where most of the faunal remains were recovered. First, Unit 10, also known as the "Yellow Brick Road," was found on both sides of the excavation, providing a clear tie point between the two packages of sediment. In the lake-margin sediments, it occurs within the Upper Silt, above the Primary Debris Flow. Second, at Locality 49, Unit 8 sits directly on top of the Primary Debris Flow, which can be traced throughout the lake-margin area. Finally, poorly sorted sand and gravel interbeds in Unit 7 appear to correlate with the coarse-grained Main Floor unit further to the east, providing a third,

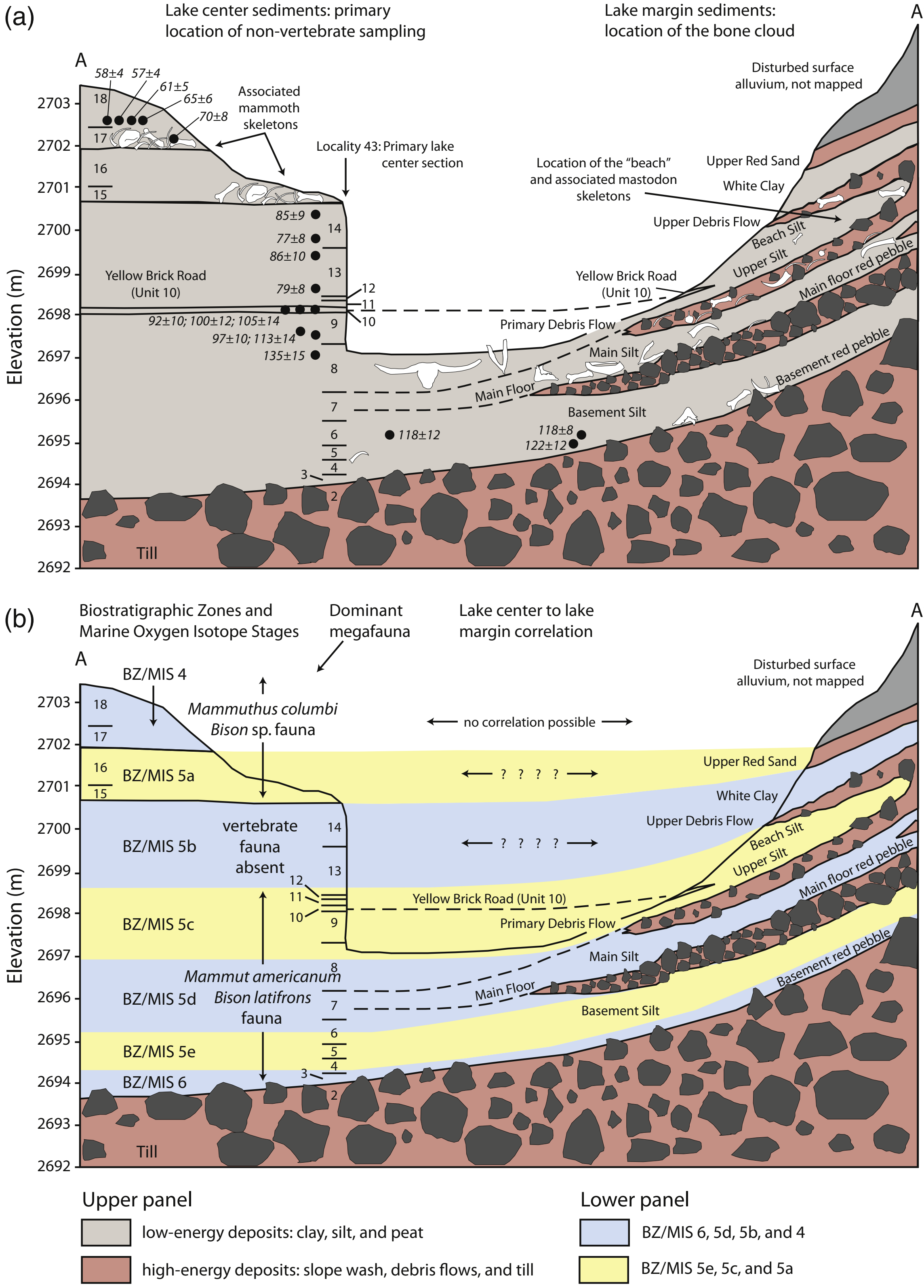

Figure 4. Generalized stratigraphic panel diagram of the Ziegler Reservoir fossil site (ZRFS) redrawn from Pigati et al. (2014-in this volume). Panel (a) shows the approximate extent of the lake-center (left side) and lake-margin (right side) sediments as they were found when scientists arrived on site. The dashed lines show the three stratigraphic tie points that allowed the correlation of the lake-center and lake-margin sequences. The black dots and associated italicized numbers show the locations and the ages (in ka) for 18 OSL samples discussed in the text (Mahan et al., 2014-in this volume). Panel (b) shows the stratigraphic correlation overlaid by biostratigraphic zones (BZ) after Anderson et al. (2014-in this volume) (see Table 1). The biostratigraphic zones approximate Marine Oxygen Isotope Stages (MIS) and substages, which permitted interpretation of how the fossil ecosystems preserved in the ZRFS responded to climate change. Vertical exaggeration in both panels is approximately 1.5.

albeit weaker, tie point (Fig. 4a, b). Thus, the chronologic framework established in the lake-center sediments can be directly tied to the lake-margin sediments, as well as the majority of the large vertebrate remains that were concentrated along the lake margin.

Chronology

The chronologic framework of the site was established using multiple methods, including radiocarbon (^{14}C), surface exposure dating using *in situ* cosmogenic nuclides, uranium-series dating, and optically stimulated luminescence (OSL). Bryant (1972) assigned the moraine that impounded most of the ZRFS to the Bull Lake glaciation, which is supported by geomorphologic evidence and the degree of soil development at the site (Pigati et al., 2014-in this volume). The ^{14}C ages of organics, bone collagen, and shell carbonate and a single *in situ* cosmogenic paired ^{10}Be and ^{26}Al exposure age on a boulder on the crest of the moraine suggest that the ages of the lake sediments are between >45 ka and ~140 ka [specific ages and all pertinent data for each method are given in the Supplemental information (Tables S.1–4) as well as in Mahan et al. (2014-in this volume)]. Uranium-series ages of vertebrate remains generally fall within these bounds, but extremely low uranium concentrations and evidence of open-system behavior limited their utility.

A total of 18 samples were collected at the ZRFS for OSL dating, including lacustrine sediments at localities 43, 51, and 52 ($n = 11$), sediments trapped within large tusks recovered from the Main Silt ($n = 2$), and blocks of sediment from Unit 18 at Locality 87 ($n = 4$) and from Unit 6 exposed in a deep pit east of Locality 43 ($n = 1$) (Fig. 4a). These samples span units 5 through 18, which constitute ~90% of the sedimentary sequence at the site. With the exception of one anomalously old sample (#ZR11.OSL-8), the OSL ages range from 122 ± 12 ka to 57 ± 4 ka and largely maintain stratigraphic order (Table S.4). The OSL ages were used as input data for flexible Bayesian age–depth analysis using the Bacon modeling software (modified after Blaauw and Christen, 2011). The entire sedimentary sequence ranged from 141 ± 14 ka to 55 ± 10 ka (Table 1).

Synthesis of the geologic and paleontologic data

The breadth and amount of data collected from the ZRFS provide an opportunity to characterize high-elevation environmental and ecosystem variability in the Rocky Mountains of Colorado between ~140 and ~55 ka, including all of MIS 5 (130–74 ka; Martinson et al., 1987). Anderson et al. (2014-in this volume) divided the ZRFS record into seven zones based on changes in the pollen assemblages. In the discussion that follows, we organize the stratigraphy and corresponding environmental proxies using the same zonation scheme (Table 1), with the exception of referring to them as “Biostratigraphic Zones” rather than “Pollen Zones” in order to reflect changes in all of the biota and environmental proxies, rather than just pollen (Fig. 4b). The seven biostratigraphic zones are tied to the chronology developed by Mahan et al. (2014-in this volume), which provides numerical ages for the sediment, fossils, and environmental proxies at the site and allows us to determine how the plants and animals responded to climatic changes.

In the sections that follow, we summarize the biota and corresponding geologic data for each biostratigraphic zone in order to characterize the local/regional environment as a whole during the different time periods. We then describe significant changes that occurred during the transitions between the zones to elucidate how the ecosystems, including both plants and animals, changed over time. These changes are discussed in light of the MIS record as recognized in high-latitude ice cores and deep-sea sediments. Corresponding stratigraphic units, depths, and age limits (upper and lower) for each of the zones are provided in Table 1, and a summary of the vertebrates (presence/absence) is provided in Table 2. [*Editor's note*: Rather than repeatedly referencing back to other studies in this volume, we note that the information presented below is attributable as follows: geology, stratigraphy, and climate—Pigati et al. (2014-in this volume) and Leonard et al. (2014-in this volume); chronology—Mahan et al. (2014-in this volume); vertebrates—Sertich et al. (2014-in this volume) and Fisher et al. (2014-in this volume); invertebrates—Haskett and Porinchu (2014-in this volume); Elias (2014-in this volume); Sharpe and Bright (2014-in this volume), and Krell (2014); and vegetation—Anderson et al. (2014-in this volume); Strickland et al. (2014-in this volume); Miller et al. (2014-in this volume), and Brown et al. (2014-in this volume)].

Ecosystem reconstruction

Biostratigraphic zone 6. Biostratigraphic zone (BZ) 6 is composed of the lowermost lake-center units (Unit 3 and the base of Unit 4) and a basal lake-margin bed (Basement Red Pebble) (Fig. 4b). The lowermost unit in the lake-center stratigraphy (Unit 3) consists of weakly bedded clay that immediately overlies the glacial till that forms the basin. The overlying organic-rich silt (Unit 4) marks the beginning of the long-term infilling sequence of the basin interior with clays, silts and organic matter. The lake-margin sequence in BZ 6 also includes a thin clay bed mantling large portions of the underlying till, as well as a matrix-supported diamictite (Basement Red Pebble) that thickens toward the shoreline (Fig. 4a). Modeled ages for BZ 6 range from 141 ± 14 to 138 ± 13 ka (Table 1) based in part on the cosmogenic age on a boulder on the crest of the moraine that impounded the lake (138 ± 12 ka for ^{10}Be and 129 ± 12 ka for ^{26}Al) (Balco et al., 2008) and OSL ages higher in section.

Although only a small number of fossils were found in sedimentary units corresponding to BZ 6, the megafauna includes *Bison latifrons*, *Equus* sp., *Mammut americanum*, and *Megalonyx jeffersonii* (Table 2). The small vertebrates are represented by a limited collection of fossils

Table 1
Stratigraphic zonation.

BZ/MIS[a]	Lower depth (cm)[b]	Upper depth (cm)[b]	Lake center[c]	Lake margin[c,d]	Estimated age (ka)[e]
4	215	0	17, 18	–	77 ± 4 to 55 ± 10
5a	338	215	15, 16	*Upper Red Sand*	87 ± 3 to 77 ± 4
5b	543	338	13, 14	*White Clay*	100 ± 3 to 87 ± 3
5c	704	543	8 (upper), 9, 10, 11, 12, 13 (base)	Upper Silt, Beach Silt, Upper Debris Flow	113 ± 8 to 100 ± 3
5d	902	704	6 (upper), 7, 8 (lower)	Main Floor, Main Floor Red Pebble, Main Silt, Primary Debris Flow	129 ± 10 to 113 ± 8
5e	991	902	4, 5, 6 (lower)	Basement Silt	138 ± 13 to 129 ± 10
6	1019	991	3, 4 (base)	Basement Red Pebble	141 ± 14 to 138 ± 13

[a] Biostratigraphic zone (BZ) designations are identical in age and depth to pollen zones developed by Anderson et al. (2014-in this volume) for the ZRFS. We equate these to Marine Oxygen Isotope Stages based on independent ages (Mahan et al., 2014-in this volume).

[b] Lower and upper stratigraphic depths of the biostratigraphic zones in the lake-center deposits at the ZRFS.

[c] Designations of the lake-center and lake-margin stratigraphic units; see Pigati et al. (2014-in this volume) and Supplementary Information for additional details.

[d] The lower lake-margin beds have clear stratigraphic tie points to the lake-center section as described in the text. The correlation of the upper lake-margin beds to the lake-center section is less clear because much of the section had been excavated before scientists arrived on site. Moreover, the upper lake-margin beds are shoreline deposits, and their fully subaqueous basinward expressions are not known. We have italicized those lake-margin beds for which our correlation is less certain.

[e] Ages for each biostratigraphic zone are based on the modeled ages of the corresponding lake-center sediments following Mahan et al. (2014-in this volume).

Table 2
Zonation of the ZRFS vertebrate record.

Taxon	BZ/MIS[a] 6	5e	5d	5c	5b	5a	4
Salmonidae			x	x			
Ranidae (>2 taxa)			x	x			
Ambystoma tigrinum	x	x	x	x		x	x
Serpentes (2 taxa)	x	x	x	x			
Lacertilia (2 taxa)			x				
Anas sp.	x		x				
Anser sp.			x				
Anatidae (4 taxa)		x	x	x			
Phasianidae			x				
Gruidae			x				
Fringillidae			x				
Charadriiformes				x			
Sorex sp. (2 taxa)		x	x	x			x
Megalonyx jeffersonii	x	x	x				
Lontra canadensis				x			
Ursus sp.		x					
Canis sp.			x				
Leporidae	x	x	x	x			
Tamias cf. *minimus*			x	x			
Tamias cf. *umbrinus*			x				
Callospermophilus cf. *lateralis*			x				
Urocitellus elegans		x	x	x			
Glaucomys cf. *sabrinus*		x	x				
Thomomys sp.			x				
Geomys sp.			x				
Castor canadensis		x					
Dipodomys sp.			x				
Neotoma sp.				x			
Peromyscus sp.	x		x	x			
Neotominae			x				
Ondatra zibethicus		x	x				
Myodes sp.		x	x	x			
Microtus sp.		x	x	x			
Synaptomys cooperi	x						
Zapus princeps		x	x				
Zapus sp.				x			
Equus sp.		x					
Camelops sp.		x				x	
Cervidae			x			x	
cf. *Odocoileus* sp.			x				
Caprinae			x				
Bison latifrons	x	x	x	x			
Bison sp.						x	
Mammut americanum	x	x	x	x			
Mammuthus columbi						x	x

[a] Biostratigraphic zone (BZ) designations are identical in age and depth to pollen zones developed by Anderson et al. (2014-in this volume) for the ZRFS and are approximately equivalent to Marine Oxygen Isotope Stages based on independent ages (Mahan et al., 2014-in this volume).

attributable to ducks, field mice, rabbits, lemmings, tiger salamanders, and snakes. Beetle, mollusk, ostracode, or plant macrofossils were not found in BZ 6. Chironomids are present, but the diversity of the assemblage is low (mainly *Corynocera oliveri* type) and nearly all of the remains are disarticulated.

The pollen composition of the sediments in BZ 6 is dominated by *Artemisia* sp., which makes up as much as 60% of the total. The arboreal pollen percentage is low (~20%), and the spruce-to-pine ratio (S:P) is <0.3. This pollen assemblage indicates that the ZRFS may have been at or slightly above tree line and surrounded by steppe-like, alpine vegetation or at most spruce krummholz at this time.

The low diversity of chironomids and the dominance of the taxon *C. oliveri* type imply a cold, deep lake in BZ 6. The midge-inferred mean July air temperature (MJAT) is 9.0°C at 1006 cm (~139 ka), which is well below present-day temperatures. (For reference, the modern MJAT at the site is 15.4°C.) The relatively low diversity of mega- and microfauna from BZ 6 is consistent with a comparatively cold climate and the presence of alpine vegetation.

Finally, the disarticulated nature of the chironomids suggests a high-energy environment, potentially due to glacial meltwater influx and/or increased sedimentation. This is supported by the fact that we interpret the lowermost stratigraphic lake-center and lake-margin beds to consist partially of rock flour that was either derived from the Bull Lake glacier that enclosed the lake basin or was blown in from nearby areas. The lake-margin diamictite is indicative of frequent reworking due to multiple, small subaqueous slope failures.

Biostratigraphic zone 5e. The lake-center sediments in BZ 5e include three organic-rich beds (most of Unit 4, all of Unit 5, and the lower half of Unit 6) (Fig. 4b) that vary from occasionally laminated silts with some clay to massive silty clay units. The lake-margin beds also consist of silts and exhibit high organic matter content. Direct OSL ages of the sediments combined with modeling indicate that BZ 5e ranges in age from 138 ± 13 to 129 ± 10 ka (Table 1).

Camelops sp. *Equus* sp., and *Ursus* sp. are found in BZ 5e along with *B. latifrons*, *M. americanum*, and *M. jeffersonii* (Table 2). Most of the additional faunal occurrences in BZ 5e are rodents, including *Castor canadensis* (North American beaver). The *M. americanum* assemblage consists of multiple juveniles and one adolescent male. In all, the number of vertebrate taxa is nearly double that of BZ 6, even though the number of fossils recovered is nearly the same. With regard to the invertebrates, the fossil beetles are represented by 14 aquatic and upland taxa, and the chironomids include occurrences of *Glyptotendipes* and *Chironomus* at the base of this zone. No ostracodes were recovered. However, one terrestrial gastropod, *Oreohelix subrudis*, as well as aquatic mollusks *Gyraulus parvus*, *Stagnicola caperata*, *Planorbella subcrenata*, *Physa* sp., and the bivalve *Pisidium nitidum* were recovered from Unit 6.

Sediments in BZ 5e contain ~40–70% arboreal pollen, with an abundance of *Quercus* sp. and *Pseudotsuga* sp., increased amounts of *Picea* and *Pinus* grains, and an S:P ratio of ~0.9. The plant macrofossil record also indicates a diverse assemblage of conifers including *Picea engelmannii*, *Pseudotsuga menziesii*, *Abies* sp., and an indeterminate but distinguishable species of *Picea*, as well as deciduous trees and shrubs (*Crataegus erythropoda* type, *Cornus sericea* ssp. *sericea*, and cf. *Quercus gambelii*) and aquatic/wetland taxa.

Oxygen isotope values ($\delta^{18}O$) of structural carbonate in mastodon tusk dentin from this zone average 22.0‰ (VSMOW) and show peak values in tusk layers formed in the spring and lower values in layers formed in autumn. Nitrogen isotope values ($\delta^{15}N$) of tusk dentin collagen average 3.6‰ (air-N_2) and exhibit seasonal variation that is in-phase with the oxygen isotope profiles, yet dentin collagen carbon isotope values ($\delta^{13}C$), which average −18.9‰ (VPDB), show little variation. One way to characterize variability within growth series is to calculate an index known as mean sensitivity. Scaled between 0 and 2, this reflects the average proportional change in thickness from one increment to the next within a series. Mean sensitivities calculated from annual growth increment series in four mastodon mandibular tusks from BZ 5e average 0.06—a low value that would imply a level of variability in growth conditions that would not be considered stressful.

The plant and beetle records indicate that the surrounding landscape was well vegetated and consisted of a dense spruce forest with a local abundance of oak and other deciduous trees or shrubs and Douglas-fir. This is corroborated by plant macrofossils that indicate a montane, mixed-conifer forest similar to present-day vegetation found at the site and at lower elevations near the ZRFS, which in turn, indicates that conditions were likely as warm or slightly warmer than present. The aquatic/wetland plant macrofossils, mollusks, and beetles also indicate a shallow-water setting and very productive ecosystem compared to other time horizons preserved in the lake. Finally, the fossil vertebrate record implies a productive ecosystem in a warm climate, matching the inferences from the geologic and fossil plant and insect data.

Temperature estimates using the Mutual Climatic Range (MCR) method for the fossil beetles indicate a maximum temperature (TMAX) of 15–17°C. These are slightly warmer temperatures than today and corroborate the implication of a somewhat warmer climate derived from the plant macrofossils. Similarly, the presence of *Glyptotendipes* and *Chironomus* midges suggests warm and productive conditions in the lake and a MJAT of 10.4°C.

The lake-center and lake-margin sediments both indicate more or less quiet-water deposition. Sedimentological indicators (grain size, sorting) show that lake-center sediments were likely influenced by reworked, subaqueous flows from the lake margin. However, the tight equivalent-dose distributions of most of the OSL samples measured indicate that much of the sediment was dust and that it was deposited in the lake via eolian transport and subsequent quiet-water deposition.

Overall, the ecosystem preserved in the ZRFS during BZ 5e was relatively productive compared to other time periods at the site. The landscape was well vegetated, and the climate was likely warmer than today. Mastodons living near the lake at this time likely experienced little to no stress due to variation in physical factors in the environment.

Biostratigraphic zone 5d. The lake-center sediments in BZ 5d consist primarily of organic-rich silts (upper half of Unit 6, all of Unit 7, and the lower half of Unit 8) except for in Unit 7, where the presence of sand and gravel interbeds appears to correlate with the Main Floor closer to the lake margin (Fig. 4a, 4b). The Main Floor is a clast-supported diamictite that thickens and coarsens markedly toward the basin margin where it eventually becomes indistinguishable from the till. Many of the rock clasts in this unit are oriented and slightly inclined toward the center of the basin and range in size from a few centimeters up to 1 m in diameter. Interestingly, there were very few large fossils recovered from this unit. Overlying the Main Floor near the basin margin are two organic-rich silt units that grade from an abundance of matrix-supported pebbles (Main Floor Red Pebble) to more or less pure silt and organic matter (Main Silt). These two units contain the most bones from megafauna of any section in the ZRFS. Finally, the uppermost unit assigned to the lake-margin beds in BZ 5d is another diamictite (Primary Debris Flow) (Fig. 4a) that is similar in appearance to the Main Floor. However, the Primary Debris Flow is matrix supported, consists of randomly oriented clasts, and exhibits a contact with the underlying Main Silt that is sharp and irregular and contains ball-and-pillow structures, indicative of rapid deposition. The age of BZ 5d ranges from 129 ± 10 to 113 ± 8 ka (Table 1).

In addition to being the most fossil rich in terms of large fossil bones (more than 1500 individual *M. americanum* bones have been identified from this zone alone; Figs. 2c and 3), BZ 5d is also the most taxonomically diverse. The megafauna include *B. latifrons*, *M. americanum*, *M. jeffersonii*, and the first appearance of cf. *Odocoileus* sp. (deer). Smaller vertebrates also show a dramatic increase in diversity, and include numerous types of birds, frogs, fish, and rodents (squirrels, rats, mice and voles). BZ 5d also produced significant numbers and diverse assemblages of ostracodes and mollusks. However, beetles were absent, and only one chironomid head capsule was recovered from units corresponding to this zone.

Mastodon tusk dentin δ^{18}O values in BZ 5d average 23.1‰ and show a peak in spring and low values in autumn. The δ^{15}N values of tusk collagen average 4.4‰ and are in-phase with the oxygen isotope profile, yet the collagen δ^{13}C values, which average −19.1‰, are relatively invariant, similar to results from BZ 5e. Mean sensitivities calculated from growth increment series for 15 tusks average 0.08.

In all measures of the floral composition, the vegetation preserved in the ZRFS record for BZ 5d is similar to that in BZ 5e, with only a slight increase in non-arboreal pollen and a slight decrease in *Quercus* pollen. As for the vertebrate record, BZ 5d contains the most diverse macrofossil flora preserved in the section. The only exception is a small decrease in the diversity of some of the aquatic/wetland macrofossils in Unit 7. As with BZ 5e, the plant record suggests that during BZ 5d, the ZRFS was not only surrounded by a montane, mixed-conifer forest of *Picea*, *Pseudotsuga*, *Quercus* and other deciduous trees similar to the modern vegetation in the region, but also included the first appearance of *Abies concolor* and a rich herb, aquatic/wetland flora with taxa that today tend to be found at lower elevations. Within the lake, the aquatic/wetland plant macrofossils again show a comparatively very productive, shallow-water ecosystem.

Ostracodes, primarily *Potamocypris unicaudata* and *Fabaeformiscandona rawsoni*, were recovered in BZ 5d from the lower part of Unit 8 (they were absent from Unit 7). Terrestrial gastropods, *O. subrudis* and *Discus* sp., as well as aquatic mollusks *G. parvus*, *P. subcrenata*, *Physa* sp., and the bivalves *P. nitidum* and *Pisidium casertanum* were recovered. Terrestrial mollusks indicate shaded, forested slopes with rotting leaves and grass. Aquatic taxa suggest a permanent, shallow water body with a muddy substrate and clear water.

Similar to the aquatic/wetland plant macrofossils, the aquatic ostracode, gastropod, and mollusk assemblages indicate the ZRFS was a well-vegetated, shallow wetland or pond with a muddy substrate. Terrestrial mollusks show that areas near or bordering the wetland were moist, shaded, and well vegetated with ample forest-floor litter. High $\delta^{18}O_{OST}$ (the OST subscript refers to δ^{18}O values from ostracode carbonate) values suggest that the ZRFS was seasonally or annually variable, with substantial evaporation. However, several ostracode taxa indicate low total dissolved solids (TDS; ~200–1000 mg L^{-1}) and more stable environments suggesting that groundwater inflow at certain areas around the ZRFS basin provided fresh, cold water to the pond. High $\delta^{13}C_{OST}$ values suggest that the site was equilibrated with atmospheric CO_2, subjected to photosynthetic enrichment of its dissolved inorganic carbon (DIC) pool, and possibly influenced by anaerobic production of methane. The mollusk and ostracode faunas do not show any appreciable change throughout BZ 5d suggesting that physical conditions did not vary significantly. This may indicate that the entire lake was hydrologically buffered.

Finally, the lake-center sediments in BZ 5d show quiet-water deposition that was occasionally influenced by sediment flux from the lake margin. The lake margin sequence implies that the lake shallowed at the beginning of BZ 5d as demonstrated by a winnowed, slope-wash bed (Main Floor), which was followed by a deepening lake and long-term quiet-water deposition as indicated by the overlying units (Main Floor Red Pebble and Main Silt). Sediments corresponding to BZ 5d are capped by the Primary Debris Flow, which was emplaced rapidly, under subaqueous conditions, based on the presence of the ball-and-pillow structures.

Overall, the sediments, fossil plant, and vertebrate and invertebrate data imply an ecosystem similar to that of BZ 5e persisted through BZ 5d under temperatures that were as warm or possibly warmer than today. As with the $\delta^{18}O_{OST}$ values, the oxygen and nitrogen isotopic compositions of tusk dentin and collagen, respectively, of *M. americanum* indicate seasonal variation, but the low mean sensitivities from annual growth increment series on tusks imply little interannual variability.

Biostratigraphic zone 5c. The lake-center units in BZ 5c (upper half of Unit 8, units 9–12, and the base of Unit 13) (Fig. 4b) are composed almost entirely of silt with variable amounts of organic material and clay. They range from laminated to massive, and vary in color from dark or light gray, to mottled brown and black, to yellowish brown. The lake-margin units consist of thick silt beds (Upper Silt and Beach Silt) that host abundant vertebrate fossils and large pieces of wood, including numerous whole logs. Many of the logs and larger pieces of wood associated with the Beach Silt were oriented parallel to the basin margin, including a few logs that are >10 m in length. The Beach Silt is overlain by a matrix-supported diamictite (Upper Debris Flow) that is sparsely fossiliferous (Fig. 4a). The age of BZ 5c ranges from 113 ± 8 to 100 ± 3 ka (Table 1).

Approximately 63 identified elements of *M. americanum* were found in BZ 5c sediments, including bones of juveniles as well as adult females and males. *B. latifrons* is the only other megafaunal taxon present. Many smaller vertebrates were found in BZ 5c, such as birds, trout, frogs, rodents, and notable first appearances of shore birds, jumping mice, woodrat, and river otter. The diversity of the smaller vertebrates in BZ 5c was less than in the units below, whereas the megafaunal diversity remained approximately the same, even though the amount of sediment available to be excavated in BZ 5c was considerably less than in BZ 5d.

The pollen and plant macrofossil record shows that a diverse and somewhat temporally varying flora was present near the ZRFS during BZ 5c. The overall pattern is of an increasingly dense *Picea* forest with an S:P ratio approaching 1.6, and corresponding declines in *Quercus* sp. and presence of *Juniperus* in the immediate vicinity. There is also a decrease in aster family pollen though BZ 5c. The later part of BZ 5c is characterized by a significant increase in *Abies* pollen up to levels only recorded in the immediate vicinity of the site today. Finally, the spore spectra show high percentages of *Pediastrum* and a notable increase in *Botryococcus* toward the end of BZ 5c. The plant macrofossil record is similar to the pollen spectra and indicates that the flora during BZ 5c continued to be exceptionally diverse, as it was during BZ 5d. Fossil cones representing *P. menziesii* and *A. concolor* were found in the same beds as fossil logs identified as *Pseudotsuga* sp. and *Abies* sp. Ring widths for four logs (three *Pseudotsuga* sp. and one *Abies* sp.) from the Beach Silt in the upper part of BZ 5c were cross-dated against each other and showed annual variations similar to those of trees living in the region today.

Diverse aquatic mollusk and ostracode assemblages were recovered from the lower portion of BZ 5c (units 8–11) indicating a shallow, productive wetland. In contrast, there was low recovery of chironomid head capsules from the sediments of this zone, but the taxon present, *Glypotendipes*, is indicative of productive conditions. Later in BZ 5c, the ostracode assemblage transitions from a *F. rawsoni* and *Potamocypris*-dominated to a *Fabaeformiscandona* sp. A and *Limnocythere herricki*-dominated fauna, and midge assemblages included *Chironomus*, *Dicrotendipes*, and *Tanytarsus* spp. Fossil beetles in BZ 5c are represented by 23 aquatic, riparian and upland taxa.

The interior of the lake basin was characterized by subaqueous, quiet-water deposition throughout BZ 5c. This is supported by the tight distribution of OSL equivalent-dose data, which suggests that much of the lake-center sediment was dust that was transported to the basin via eolian processes. The presence of oxidized iron species in Unit 10 (a yellowish-brown silt) indicates that the lake may have shallowed significantly at ~100 ka. The pollen, plant macrofossils, aquatic invertebrates, and lake-margin debris flow-type deposits also suggest lower lake levels at this time. Whether related or not, it appears that a potentially catastrophic event occurred near the top of the Beach Silt, where time series from seven logs show a possible synchronous mortality event.

Overall, the plant, insect and aquatic and terrestrial invertebrate assemblages indicate that the vegetation around the ZRFS consisted of a moderately dense, shaded and partially closed, montane, mixed-conifer forest with decreasing oak populations but ample forest-floor litter and more herbaceous vegetation compared to earlier times at the lake. The continued presence of *A. concolor*, *P. menziesii*, *P. engelmannii*, and a second indeterminate *Picea* species along with deciduous and other plant taxa found at lower elevations today, as well as annual ring width variations of four cross-dated trees from the Beach Silt that are similar to trees living in the region today, indicate that temperatures as warm as or warmer than modern and wet conditions prevailed at this time.

Within the lake, the aquatic/wetland plant macrofossils and the aquatic invertebrates indicate a shallow-water setting and very productive ecosystem. The aquatic ostracode and mollusk assemblages recovered from the lower portion of BZ 5c (units 8–11) show that the ZRFS was a well-vegetated, shallow wetland with a muddy substrate and submerged and emergent vegetation. Ostracode and mollusk assemblages indicate that the wetland was fed by fresh, cold-water springs, yet high $\delta^{18}O_{OST}$ values in Unit 8 indicate that the ZRFS was likely subjected to substantial evaporation. High $\delta^{13}C_{OST}$ values suggest that the site was (nearly) equilibrated with atmospheric CO_2, subjected to photosynthetic enrichment of its dissolved inorganic carbon (DIC) pool, and possibly influenced by the anaerobic production of methane. The mollusk and ostracode faunas do not show any appreciable change from BZ 5e through BZ 5c, suggesting that physical conditions in the wetland did not vary significantly, which may indicate that the entire lake was hydrologically buffered.

The estimated midge-derived average MJAT for BZ 5c is ~10.2°C. However, as with the plant macrofossils and pollen, notable variation occurred within BZ 5c, including a spike and subsequent drop in MJAT of ~1°C in the upper half of the zone. A somewhat warmer MCR estimate based on the fossil beetles gives a TMAX of 13–16°C, which is about 0.5–3.5°C below modern temperatures. There is a transition of the ostracode assemblage toward the end of BZ 5c, which indicates increased surface or groundwater flow or a higher rate of throughflow, reduced TDS, and possibly colder and deeper water within the basin.

Taken with the geologic and fossil plant, vertebrate, and invertebrate data, all the proxies suggest that on average, the ZRFS was probably as warm as today, and supported a productive, stable ecosystem at this time. Exceptions are the fluctuations in plant composition and shifts in temperature as inferred through midges and beetles, and, toward the end of BZ 5c, a lake-lowering event as inferred by sedimentology and a spike in *Pediastrum* and *Botryococcus*, and the onset of ostracode turnover above Unit 11. Notably, *M. americanum* and *B. latifrons*, and all deciduous tree and shrub taxa, are absent above this biostratigraphic zone.

Biostratigraphic zone 5b. The lake-center section in BZ 5b consists of two, relatively thick, silty clay units that are composed mostly of silicates, and range from bedded (Unit 13) to massive (Unit 14) (Fig. 4a, b). The lake-margin beds are most complex in the upper portions of the section. Most of the sediments that correspond to BZ 5b were removed by contractors before scientists arrived on site, which complicated stratigraphic correlation of the lake-center and lake-margin units. As such, the basinward expressions of these lake-margin beds were not documented and thus, their stratigraphic correlation is tentative (Fig. 4b). We assign only the White Clay, which did not contain any mega- or microfaunal remains, to BZ 5b. Modeled ages of BZ 5b range from 100 ± 3 to 87 ± 3 ka (Table 1).

The pollen spectrum in BZ 5b is dominated by *Artemisia* sp., which makes up as much as 60% of the total and shows marked increases in grasses, Amaranthaceae, and greasewood. The percentage of arboreal pollen is low (<20%), and the S:P ratio is often <0.3 and sometimes <0.2. The spore spectrum also shows high percentages of *Botryococcus*. A change in the plant macrofossil record also occurs in BZ 5b. Tree taxa disappear near the beginning of the zone and only aquatic/wetland taxa are found. Cones were not found in this zone.

The upper portion of BZ 5b is devoid of chironomid remains; however, the sediments at the very base of BZ 5b contained abundant midge head capsules. The ostracode assemblage is dominated by *Fabaeformiscandona* sp. A and *L. herricki*, and the mollusk bivalve *Pisidium millium* is present in Unit 14. Eighteen fossil insect taxa were found, including several high-latitude or high-elevation, tree line, or even snowfield taxa (e.g., *Bembidion breve*, *Elaphopus incurvus*, and numerous species of *Tachinus*). The inferred TDS values from ostracodes and mollusks, as well as the $\delta^{18}O_{OST}$ and $\delta^{13}C_{OST}$ values, are lower than the older zones.

The interior of the lake basin continued to be dominated by quiet-water deposition in BZ 5b. Similarly, the lake-margin bed is indicative of slow and potentially quiet-water deposition. Fossils were not recovered from the lake margin. In contrast to the older zones, proxy data in the lake center, including pollen, insects and aquatic invertebrates, suggest that very cool (and potentially dry, in the case of pollen) conditions, possibly with colder, deeper water, increased ground- or surface-water flow, and reduced TDS, prevailed during BZ 5b. The pollen spectra suggest spruce-krummholz or even alpine vegetation and that the site was at or near tree line. This is supported by the chironomids, which appear only at the base of BZ 5b and indicate a MJAT of only 9.6°C. The absence of midge remains throughout the rest of BZ 5b may reflect the presence of extended or permanent ice cover through the growing season at the ZRFS. Many of the fossil insect taxa in BZ 5b are found today only at higher elevations, higher latitudes, or along snowfields, and indicate a TMAX of 10–14°C, which is well below modern temperatures. The presence of *L. herricki* (ostracode) and *P. millium* (aquatic bivalve) also indicates cold environments as these taxa have modern ranges that extend into the Canadian prairies and the Aleutian Islands and Great Slave Lake, respectively [see Sharpe and Bright (2014-in this volume) for the ranges of these taxa].

Overall, the geologic and fossil proxies from sediments suggest that the ZRFS environment was cold and the site was positioned at or near tree line during BZ 5b. The ecosystem was not nearly as productive or stable as in previous zones, based on both the lower diversity of the whole faunal and floral assemblage and the absence of entire groups (e.g., vertebrates from all of BZ 5b; chironomids and tree macrofossils from most of BZ 5b). Finally, although the pollen data suggest that the environment might have also been much drier, other proxies indicate that much cooler and wetter conditions prevailed.

Biostratigraphic zone 5a. Sediments comprising BZ 5a are almost entirely limited to the center of the lake basin, and include a peaty silt (Unit 15) that grades up into peat (Unit 16). Although the underlying peaty silt contains bedded vegetation, the peat is massive and contains very little mineral matter. The lone lake-margin unit that falls within BZ 5a is a well-sorted, massive red sand near the top of the near-shore sedimentary sequence (Fig. 4a). OSL ages were not obtained from any of these units. One sample from a bison femur has a possible age, based on U-series dating, of 49 ± 7 ka for Unit 15 (Table S.3), although evidence of open-system behavior in many of the samples submitted for U-series dating limits the confidence we have in this particular age. Based on the age-depth model, BZ 5a falls between 87 ± 3 and 77 ± 4 ka (Table 1).

The vertebrate fossils in BZ 5a all come from Unit 16 and include *Camelops* sp., *Bison* sp., the first appearance of *Mammuthus columbi*, and an unidentified member of the Cervidae family. Smaller vertebrates are limited to the ubiquitous tiger salamander (*Ambystoma tigrinum*). Although ostracodes and gastropods were not found, fossil chironomids and insects are common to abundant in BZ 5a. The largest shift in midge community composition occurs during the transition from Unit 15 to Unit 16. Midges in Unit 15 consist primarily of taxa indicative of productive lake conditions including *Glyptotendipes*, *Chironomus*, *Dicrotendipes*, and *Tanytarsus* spp., whereas midges in Unit 16 consist of semi-terrestrial and terrestrial taxa such as *Limnophyes*/*Paralimnophyes* and *Smittia*/*Parasmittia*. Twenty-five species of insects occur in BZ 5a, including species indicative of aquatic, riparian, and upland environments.

The pollen assemblage from BZ 5a is characterized by high percentages of arboreal pollen, particularly *Picea*. The S:P ratio is also higher than any other point in the ZRFS section, with samples exceeding values of 1.6. High percentages of Cyperaceae and progressively decreasing amounts of *Quercus* through the zone were observed. The plant macrofossils during this time include *P. engelmannii*, *P. menziesii*, and *Pinus flexilis*, but those of deciduous trees are absent. *Najas flexilis* fruits and abundant bryophytes are found within the peat.

The sedimentary succession during BZ 5a indicates a shallowing of the lake as it transitioned from an open body of water to a reed-dominated (along the basin margin), peat-forming marsh. This interpretation is supported by the distinct transition in midge (including Ceratopogonidae) and insect taxa, and the presence of reed pollen and seeds of *Schoenoplectus acutus* var. *acutus* (bulrush/tule) and abundant bryophytes. The high percentage of arboreal pollen and a very high S:P ratio indicate a closed spruce forest. The fossil insect fauna supports a dense forest interpretation but also indicates the presence of pine, Douglas-fir, and juniper in the immediate vicinity of the lake. The MCR reconstruction of TMAX based on the insects is 15.5–17.5°C, which is within 1°C of modern temperatures. The midge-inferred MJAT gradually increased through BZ 5a, reaching a maximum of 13.3°C, which is the warmest inferred temperature of the entire ZRFS record. Overall, the ZRFS ecosystem during BZ 5a time appears to be productive and stable and marks the beginning of the second megafaunal assemblage as defined by the presence of *M. columbi* and *Bison* sp. (Fig. 4b).

Biostratigraphic zone 4. Biostratigraphic zone (BZ) 4 is the uppermost zone represented in the ZRFS section and includes two lake-center units that consist of relatively thick clays with varying amounts of silt and organic material (units 17 and 18) (Fig. 4a). Chronologic data from these units include three radiocarbon ages, two obtained from dentin collagen and bone collagen from the Clay Mammoth [see Fisher et al. (2014-in this volume) for details about this specimen], and one age obtained from humic acids near the specimen. Only the dentin collagen returned a plausible age of 46.2 ± 1.9 ka (Table S.1). One aliquot of gastropod shell fragments in the lower part of Unit 18 yielded an age of 44.3 ± 1.9 ka. Because ^{14}C activities in these samples are either at or near background levels, we consider both of these to be minimum ages. Four OSL samples in Unit 18 showed a progression from 65 to 57 ka (Table S.4) but the equivalent-dose results are more scattered than in older units, indicating a possible mixture of sediment transport mechanisms. Finally, one OSL sample in Unit 17 showed an equivalent-dose dispersion of 14% and returned an age of 70 ka, which is the second highest dispersion of any OSL sample analyzed from the section. The age–depth model indicates that the age of BZ 4 ranges from 77 ± 4 to 55 ± 10 ka (Table 1).

Compared to the other zones, very few fossils were found in BZ 4. The vertebrate fauna consisted of one shrew taxon, tiger salamanders, and *M. columbi*. However, we note that the Clay Mammoth specimen is of particular interest as the circumstances of its death and subsequent deposition are unusual. The specimen consists of a partially articulated skeleton of a large male that was found in the middle of the lake basin in a low-energy depositional environment. The skeleton was under- and overlain by more than 20 cobbles and boulders, many of which are >10 kg. Presently, no clear depositional mechanism for the accumulation/association of the rocks and partial skeleton has been identified. Investigations of this specimen and its depositional circumstances are ongoing.

Unit 18 produced only one chironomid head capsule from the genus *Zavreliella*, one intact ostracode valve, *F.rawsoni*, and some unidentified mollusk shell fragments. Neither fossil insets nor plant macrofossils were recovered from this zone. The pollen spectrum shows a considerable increase in non-arboreal pollen, particularly *Artemisia*, an S:P ratio of about 1.0–1.2, and the highest levels of Cyperaceae anywhere in the record.

Sediments in units 17 and 18 represent the final infilling of the ZRFS marsh and the formation of a wet meadow. The OSL dates from the middle of the basin indicate that some of the sediments may have been deposited via a combination of fluvial or alluvial processes, along with the ubiquitous eolian sediments. Although limited, the midge data reflect the presence of submerged macrophytes in shallow water. The pollen spectrum and the S:P ratio suggest that the forest surrounding the ZRFS was a mosaic of subalpine spruce and pine with abundant sagebrush, indicating cooler and drier conditions than BZ 5a.

Climate transitions at the ZRFS and comparison to regional and global records

Ecological responses during stadials and interstadials of MIS 6/5/4 at mid-latitudes in the terrestrial realm are known from only a few deposits in North America. Among others, these include Bear Lake, Owens Lake, Carp Lake, Clear Lake, Hybla Valley, and several marine sites off the Pacific and Atlantic Coasts (Adam et al., 1981; Adam and Robinson, 1988; Whitlock and Bartlein, 1997; Heusser, 2000; Lyle et al., 2001; Pisias et al., 2001; Heusser and Oppo, 2003; Woolfenden, 2003; Jiménez-Moreno et al., 2007; Kaufman et al., 2009; Litwin et al., 2013). These studies generally found a correlation of terrestrial climate and ecological-proxy data, particularly the pollen records, with data from the deep-sea and ice-core records. This suggests that a global (or at least hemispheric) coupling of the ocean–atmosphere system and continental-scale teleconnections between climate, ice-volume, sea-surface temperatures, deep water production, ice-sheet configuration, and summer insolation prevailed during the late Pleistocene (e.g., Kukla et al., 2002).

The paleontological record from the ZRFS also suggests strong coupling to global atmospheric and oceanic circulation patterns during MIS 6/5/4 but with a few surprises as discussed below (Table 3; Fig. 5). Because of the inclusion of assigned ages in the upper part of the stratigraphic section [see the chronology section in the Supplemental information, as well as Mahan et al. (2014-in this volume) for details], we do not interpret time leads or lags in the ZRFS record compared to other records, but instead correlate our biostratigraphic zones to Marine Oxygen Isotope Stages and substages and interpret the transitions between the zones and the overall conditions within each zone at the ZRFS itself. Thus, for the sake of simplicity in this section, we use MIS designations and abandon the biostratigraphic zone terminology for the remainder of this section (Table 1).

The earliest sediments in the ZRFS were deposited during the end of MIS 6. Similar to vegetation and climate records that date to the end of MIS 6 elsewhere in North America (e.g., Heusser, 1995; Woolfenden, 2003; Jiménez-Moreno et al., 2007), the ZRFS record indicates that cold, dry, and low-productivity conditions prevailed at this time. The MIS 6 pollen spectra at the ZRFS closely resemble those that have been interpreted as representating alpine tundra from MIS 2 sites elsewhere in the Rocky Mountains (Jiménez-Moreno et al., 2011; Jiménez-Moreno and Anderson, 2012; Anderson et al., 2014-in this volume).

The transition from MIS 6 to MIS 5e in the ZRFS was fast (i.e., sub-millennial) and dramatic, similar to that found in most regional and global records. At the ZRFS, the elevation of the upper tree line increased significantly, and the site transitioned from being at or above tree line to well below it. The shift in pollen spectra at this time is strikingly similar to the MIS 2/1 transition observed in other high-elevation Rocky Mountain lakes (Anderson et al., 2014-in this volume, and references therein), with the major difference being that the ZRFS pollen record shows significantly higher-than-modern percentages of *Pseudotsuga* and *Quercus* that reach a peak in the middle part of MIS 5e. This hints at the presence of possible "no-analog" plant communities in Colorado's Rocky Mountains during MIS 5e.

Temperature estimates from the beetle and chironomid records, and the overall diversity and composition of the plant macrofossil record, confirm a very warm and productive MIS 5e. Taken together, the ZRFS paleontological record supports the idea that MIS 5e was slightly warmer than MIS 1 (e.g., Heusser, 2000; Lyle et al., 2001; Muhs et al., 2002; EPICA community members, 2004; CAPE-Last Interglacial Project Members, 2006). Importantly, it shows that the warm conditions extended to the high-elevation Rockies in the mid-latitudes of North America. In terms of inferred climate, while the MIS 6/5e transition at the ZRFS appears similar to the MIS 2/1 transition elsewhere, data representing short-term climate events similar to the Bølling-Allerød and Younger Dryas are absent despite the fact that the ZRFS sediments were sampled at a sub-millennial scale (Anderson et al., 2014-in this volume).

North American records of MIS 5e also indicate aridity in addition to warming (e.g., Jiménez-Moreno et al., 2007). The high percentages of *Quercus* in the ZRFS record indicate that conditions during MIS 5e were as dry as or drier than today. Isotopic data from structural carbonate and collagen in tusk dentin of *M. americanum* specimens are indicative of seasonality, which is not unexpected for a high-elevation habitat. However, the low mean sensitivities calculated from annual growth increment series on tusks suggest that *M. americanum* individuals experienced little interannual variability in growth conditions.

The transition between MIS 5e and 5d in the ZRFS is characterized by little to no change in any of the terrestrial and aquatic environmental

Table 3
Ecosystem interpretation for each biostratigraphic zone/Marine Oxygen Isotope Stage.

BZ/MIS (Age)	Inferred ecosystem at the Ziegler Reservoir fossil site (ZRFS)
4 (~77–55 ka)	The ZRFS was somewhat below tree line and surrounded by a mosaic of *Picea*, *Pinus*, *Abies*, *Pseudotsuga*, and *Quercus*. *Artemisia* was abundant. The forest was open but not as open as in BZ 5b. The lake transitioned from a marsh to a wet meadow. The vertebrate fauna was depauperate consisting only of *Mammuthus columbi*, tiger salamanders, and a species of shrew. All fossil proxies indicate cool and dry conditions.
5a (~87–77 ka)	The ZRFS was below tree line and surrounded by a closed conifer forest dominated by *Picea*, but with *Pinus* present. Deciduous tree or shrub taxa were absent from the local vegetation. The lake was warm, productive, and stable, and transitioned from an open body of water to a reed-dominated, peat-forming marsh. The vertebrate fauna contained *M. columbi* and *Bison* sp. instead of *Mammut americanum* and *Bison latifrons*. Beetle-inferred summer temperatures were within ~1°C of modern temperatures and midge-inferred mean July air temperature was at its highest level of the entire ZRFS record.
5b (~100–87 ka)	The ZRFS was at or slightly above tree line and surrounded by steppe-like, alpine vegetation in the spruce krummholz or alpine zone, which suggests a lowering of the tree line of 800–1000 m from BZ 5c accompanied by a significant drop in temperature. *Artemisia* pollen percentages nearly match those from BZ 6, and there is a notable increase in grass pollen. The lake was cold, exhibited low productivity and was potentially covered by ice through the midge growing season. The vertebrate fauna was non-existent in BZ 5b. Summer temperatures were well below modern levels and as cool as BZ 6.
5c (~113–100 ka)	The ZRFS was below tree line and surrounded by an increasingly dense, montane, mixed-conifer forest with potentially *Juniperus* in the immediate vicinity. High percentages of *Pediastrum* and *Botryococcus* and data from aquatic invertebrates suggest the character of the lake was shallowing and/or expanding the portions that would be considered a wetland. Cross-dated tree ring series indicate relatively warm and wet conditions prevailed. On average, the lake was warm and productive, subject to substantial evaporation, and partially fed by groundwater. The vertebrate fauna indicate warm conditions, and show no signs of seasonal stress. Summer temperatures were slightly cooler than modern temperatures. Fluctuations in plant composition, temperature, ostracode assemblages, and lake level indicate cooler and possibly wetter conditions by the end of BZ 5c.
5d (~129–113 ka)	The ZRFS was below tree line and surrounded by a moderately dense, montane, mixed-conifer forest similar to present-day vegetation found at the ZRFS but with *A. concolor* and plant taxa found today at lower elevations. *Quercus* pollen percentages were lower than BZ 5e suggesting BZ 5d was slightly cooler than the preceding period. The lake was shallow, warm, very productive, partially fed by groundwater, and may have been subject to substantial evaporation. The vertebrate fauna and plant macrofossil flora were exceptionally rich, indicative of warm conditions, and showed no signs of seasonal stress.
5e (~138–129 ka)	The ZRFS was well below tree line and surrounded by a dense, montane, mixed-conifer forest with abundant *Picea*, *Pseudotsuga menziesii*, and *Quercus* similar to present-day vegetation found near the ZRFS and at lower elevations. The lake was warm and very productive. The vertebrate fauna was rich, indicative of warm conditions, and showed no signs of seasonal stress. Summer and winter temperatures were as warm as or warmer than modern.
6 (~141–138 ka)	The ZRFS was at or slightly above tree line and surrounded by steppe-like, alpine vegetation in the spruce krummholz zone with abundant nearby *Artemisia* indicating cold and dry conditions. The lake was cold, deep and exhibited low productivity. The vertebrate fauna was depauperate and indicative of cool conditions. Summer temperatures were well below modern temperatures.

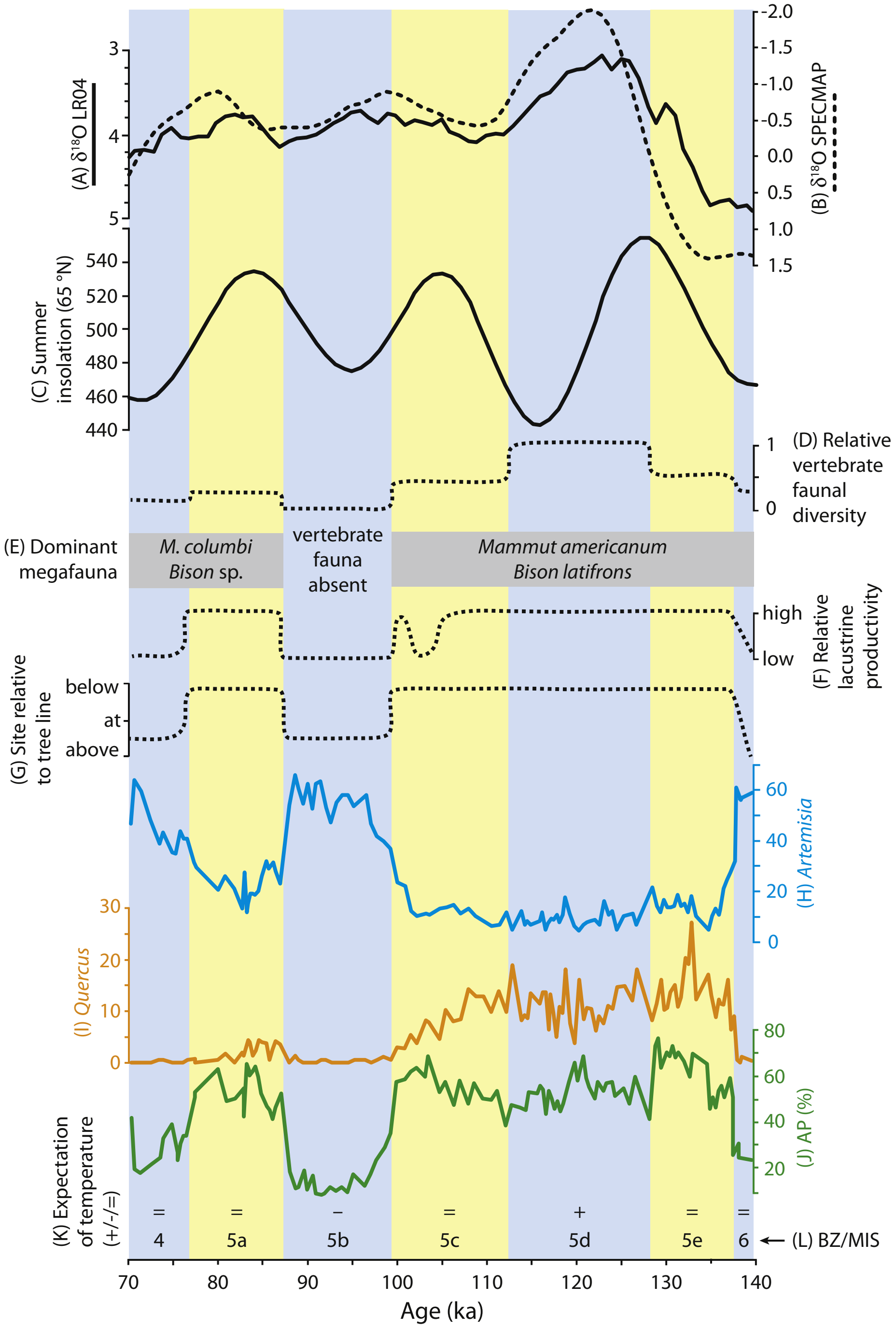

Figure 5. Multiple fossil proxies, records, and inferences from the Ziegler Reservoir fossil site (ZRFS) plotted against age. (A) $\delta^{18}O$ LR04, based on benthic foraminifera (Lisiecki and Raymo, 2005); and (B) $\delta^{18}O$ SPECMAP, based on planktonic foraminifera (Martinson et al., 1987). These marine records are plotted to illustrate global climate conditions. (C) Summer insolation at 65°N (Laskar et al., 2004). (D) Relative vertebrate faunal diversity at the site; these values were calculated by dividing the abundance of taxa in each biostratigraphic zone (BZ)/Marine Oxygen Isotope Stage (MIS) by the number of taxa in the most diverse zone/stage (in this case, BZ/MIS 5d). (E) Duration of the two dominant megafauna assemblages at the site; (F) relative lake productivity based on the abundance, diversity, composition, and chemistry of aquatic plants, insects and mollusks; and (G) elevation of the site relative to tree line based on pollen and plant macrofossils (Anderson et al., 2014-in this volume; Strickland et al., 2014-in this volume). The ZRFS pollen records for (H) *Artemisia* (blue line), (I) *Quercus* sp. (orange line), and (J) AP % (arboreal pollen %) (green line). Note that (H–J) are based on pollen data from Anderson et al. (2014-in this volume). (K) Temperatures at the ZRFS based on inferences from proxy data compared to temperature inferences for MIS substages derived from other North American sites (see text for discussion). The plus sign indicates that conditions at the ZRFS were warmer than expected, the minus sign indicates colder than expected, and the equal sign indicates that temperature estimates approximate those expected based on other sites. (L) Biostratigraphic zones/Marine Oxygen Isotope Stages and substages (yellow and blue shaded regions).

and ecological proxies. A small decrease in *Quercus* and arboreal pollen signifies that a slight opening of the forest occurred at this time, and a small decrease in aquatic macrofossil diversity suggests either a slight cooling or deepening of the lake. *A. concolor* first appears during MIS 5d at the site, suggesting warmer winters and summers than present-day conditions. In addition, the macrofossil flora continues to increase in diversity with many extra-local taxa appearing throughout this period.

The MIS 5e/5d transition at the ZRFS was muted compared to other North American terrestrial sites, but was similar to the relatively tempered transition recorded in marine settings (e.g., Heusser and Oppo, 2003). A trend toward cooler and wetter conditions characterizes other MIS 5d records, whereas all of the ZRFS paleontological proxies indicate a warm climate and highly productive lake very similar to MIS 5e. The oxygen isotopic composition of ostracode valves implies that substantial evaporation occurred at this time, and the oxygen and nitrogen isotopic composition of tusk collagen of *M. americanum* specimens indicates continuation of seasonality. Despite these patterns, the overall aquatic environment represented by the mollusk and ostracode faunas is relatively stable, and the *M. americanum* annual tusk growth increment series suggest that the animals were not appreciably stressed from climate or diet. Finally, the ZRFS vertebrate fauna (Table 2) and the vegetation, as indicated by plant macrofossils, were diverse during MIS 5d, reinforcing the implication of favorable environmental conditions.

It is unclear why the environmental and ecological responses to MIS 5d climate were so similar to MIS 5e in the ZRFS and muted compared to other MIS 5d terrestrial records in North America. The occurrence of major global environmental changes from MIS 5e to 5d, including growth of ice sheets and a significant decrease in temperature (e.g., Kukla et al., 2002; Cutler et al., 2003, but note that they could not estimate sea level during MIS 5d), should have profoundly influenced high-elevation ecosystems. The fact that the ZRFS was not appreciably affected suggests that conditions in the Rocky Mountains of Colorado may not have met the climatic threshold that would have triggered significant environmental change at high elevations. Alternatively, MIS 5d may have been relatively short and not as dramatic a period of ice growth as previously thought (Peteet et al., 1992; Sánchez Goñi et al., 1999).

The MIS 5d/5c transition at the ZRFS was also muted, again in contrast to other sites in North America. This is mostly due to the fact that MIS 5d is so similar to MIS 5e and 5c at the ZRFS, rather than a cooler-than-expected MIS 5c. The changes from MIS 5d to 5c in the ZRFS record are subtle and represented by an increasingly dense, montane, mixed-conifer forest dominated by *Picea* and increased percentages of *Pediastrum* and *Botryococcus* (Fig 6a). Although the transition between MIS 5d and 5c was different than at most sites, all proxies suggest that conditions during MIS 5c at the ZRFS were similar to other sites in North America. The climate was warm and wet and on average, the lake was warm, productive, and subject to substantial evaporation. Although MIS 5c summer temperatures were warm, they were slightly cooler than MIS 5e and modern temperatures.

The MIS 5c record in the ZRFS is characterized by fluctuations in plant composition, temperature, ostracode assemblages, and lake level. Notably, the younger half of MIS 5c shows a spike and subsequent drop in midge-estimated temperatures, a turnover in the ostracode assemblage, a lake-lowering event indicated by the sedimentology, and a spike in *Abies* pollen and *Pediastrum* and *Botryococcus*. A similar cool episode is present in Bear Lake, Clear Lake and the Santa Barbara Basin (Jiménez-Moreno et al., 2007). Jiménez-Moreno et al. (2007) and others argue that these events are linked to North Atlantic Deep Water production and the resulting cooling between approximately 105 and 100 ka (e.g., Keigwin et al., 1994). The fact that the ZRFS appears to exhibit both an environmental and ecosystem response at approximately this time [although note that the age model uncertainty is on the order of 10 ka (Mahan et al., 2014-in this volume)] indicates that strong hemisphere-scale teleconnections may have affected conditions in the Rocky Mountains. This point is particularly unusual because the ecological response at the ZRFS during MIS 5d was muted compared to that at other North American sites, which responded significantly to global climate forcing.

The transition from MIS 5c to 5b was abrupt (sub-millennial) and led to the first major and prolonged cooling in the ZRFS record since the onset of MIS 5e. Tree line dropped substantially (~800–1000 m), and the site was surrounded by steppe-like, alpine vegetation in the spruce krummholz or alpine zone for ~10,000 yr. *Artemisia* pollen percentages return to MIS 6 levels, and macrofossils of trees are absent. The ostracode, mollusk and midge records suggest very cold, low-productivity conditions in the lake prevailed during MIS 5b, and that it may have been ice covered through the midge growing season at this time. The beetle temperature estimates show a notable drop in summer temperatures to well below MIS 5c/5d/5e or MIS 1 values. Finally, mega- and microfaunal vertebrates are completely absent in units that correspond to MIS 5b (Table 2). Although comparatively little lake-margin sediment was available to excavate (see stratigraphy discussion), it is still surprising that vertebrates were not recovered.

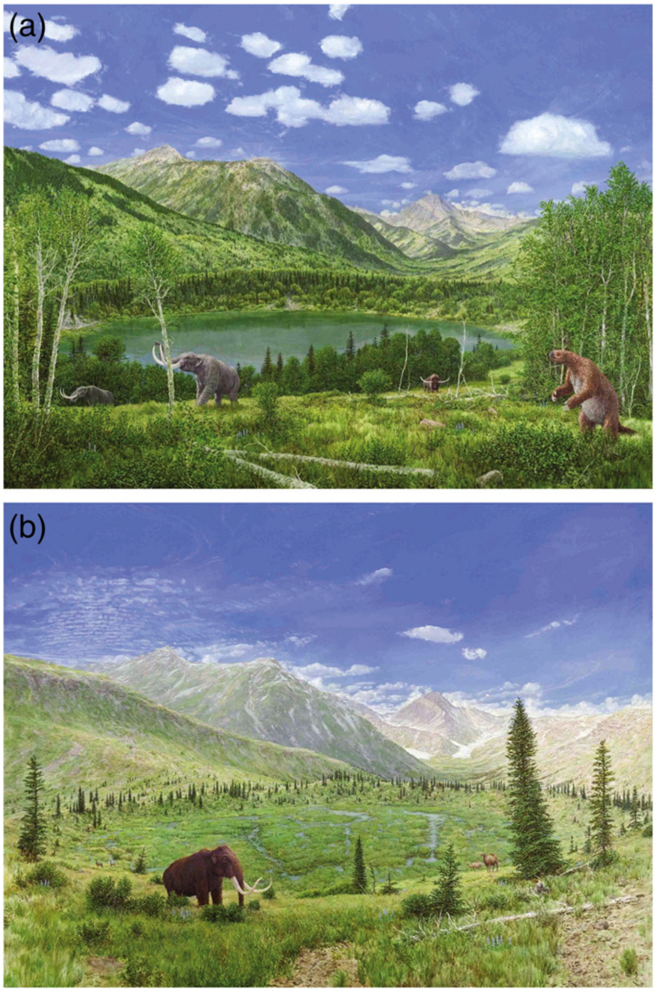

Figure 6. Paleo-landscapes showing representative fossil ecosystems present at the ZRFS during the beginning and end of the record preserved within the basin (see Johnson and Miller, 2012 for all five original paintings by Jan Vriesen). The upper painting (a) shows the site as it appeared during MIS 5e to 5c between ~135 and 100 ka. The site is below tree line and generally surrounded by a montane, mixed conifer forest; the lake is productive and warm; and the megafauna is dominated by *Mammut americanum*, *Bison latifrons*, and *Megalonyx jeffersonii*. The lower painting (b) shows the site as it appeared during MIS 4 between ~75 and 55 ka. The site is near tree line and generally surrounded by an open, *Picea*-dominated forest; the lake has become a peat bog; and the megafauna is dominated by *Mammuthus columbi* and *Bison* sp., even though a camel is depicted in the painting.

The environmental response at the ZRFS to MIS 5b climate was stronger than expected because most proxies at the site indicate that the ecosystem returned to MIS 6-like conditions. Several North American sites including Devil's Hole, Owens Lake and the Santa Barbara Basin also show that the environmental and ecosystem responses to MIS 5b were strong (Winograd et al., 1992; Coplen et al., 1994; Heusser, 2000; Woolfenden, 2003). However, these sites do not indicate that conditions returned to the extremes seen in MIS 6. Whereas MIS 5b environmental pressures on the ZRFS ecosystem might have been exacerbated because the site is at high elevation, it is unusual that the response to MIS 5d was muted, and yet the response to MIS 5b was amplified. The ZRFS record suggests that the build-up and configuration of the North American Ice Sheet (e.g., Kleman et al., 2010), and teleconnections between the Atlantic and Pacific Ocean basins during the end of MIS 5 (e.g., Reheis et al., 2012) strongly affected environments and ecosystems in the Rocky Mountains of Colorado.

The transition from MIS 5b to 5a at the ZRFS was again sub-millennial and significant, similar to the transition from MIS 6 to 5e at the site. The most dramatic trend was that tree line increased rapidly in elevation, moving well above the site as indicated by high percentages of arboreal pollen and the return of conifer macrofossils. Compared to other North American records, the MIS 5b/5a transition at the ZRFS is typical. The Clear Lake, Carp Lake and the Santa Barbara Basin records all show an abrupt transition to warmer and more arid conditions (Adam et al., 1981; Whitlock and Bartlein, 1997; Jiménez-Moreno et al., 2007). The rest of MIS 5a at the ZRFS appears climatically very similar to MIS 5e–5c time at the site, although there are no deciduous tree macrofossils, or ostracodes or mollusks, which may indicate cooler temperatures. The lake was warm and the aquatic ecosystem appears to have been productive and stable. The terrestrial ecosystem was also warm and stable with beetle-inferred summer temperatures within ~1°C of modern temperatures at the site and midge-inferred mean July air temperature was at its highest level.

The strong ecosystem response to MIS 5b at the ZRFS served to reorganize the forest and the vertebrate fauna. The average pollen spectrum during MIS 5a shows much higher percentages of *Picea* and graminoid pollen and considerably lower percentages of *Quercus* than during MIS 5e–5c. Similarly, the plant macrofossil record shows the return of all conifers that were present during MIS 5e–5c (with the exception of *A. concolor*) although none of the deciduous tree taxa returned. Along with these notable changes in the flora, the vertebrate megafauna, which was dominated by the predominantly closed-forest and browsing taxa *M. americanum* and *B. latifrons* during MIS 5e–5c, shifted to being exclusively dominated by the primarily open-grassland and grazing taxa *M. columbi* and *Bison* sp. in MIS 5a (Tables 2, 3). Given that the beetle and midge proxies indicate that the MIS 5a ecosystem was very similar to MIS 5e–5c at the ZRFS, the change in megafaunal composition appears to be linked to the corresponding shift in vegetation represented primarily by an increase in graminoids and loss of deciduous trees and shrubs in the local vegetation.

The youngest sediments in the ZRFS capture the transition from MIS 5a to MIS 4. Environmental proxies in the MIS 4 sediments are sparse and are overprinted by rooting and other soil forming processes. Nonetheless, the pollen record does show a dramatic transition to MIS 4. Though the site remained near tree line, it was surrounded by a mosaic of *Picea*, *Pinus*, *Abies*, *Pseudotsuga*, and *Quercus* with abundant *Artemisia* nearby (Fig. 6b). The megafaunal taxa remained the same as during MIS 5a. Unlike some North American records, which show the MIS 5a/4 transition as being as abrupt and dramatic as the MIS 6/5e transition (e.g., Heusser, 2000) the response at the ZRFS was more muted. With the exception of the stratigraphically highest sample in the pollen profile, MIS 4 at the ZRFS eventually approximated MIS 6 conditions.

Conclusions

The Ziegler Reservoir fossil site (ZRFS) contains an unprecedented, long-term (~85 ka), and nearly continuous record of high-elevation (2705 m) ecosystem change during the penultimate glacial–interglacial–glacial (MIS 6/5/4) cycle in central Colorado. Located immediately adjacent to Snowmass Village, CO, the site is contained in a small (14.2 ha) basin that formed during the Bull Lake/MIS 6 glaciation at the apex of a ridge between the Snowmass Creek and Brush Creek drainages. After the Bull Lake glacier receded at the end of MIS 6, the basin filled with water, creating a ~5 ha lake that slowly filled with sediment between ~140 and 55 ka, first evolving from a lake into a peat-forming swamp and ultimately into an alpine meadow.

The sediments in the ZRFS basin consist of two distinct packages: a lake-center sequence, which is dominated by eolian transport to the basin and subsequent quiet-water deposition; and a lake-margin sequence, which is characterized by bank collapse and subaqueous deposition mostly within the wave base. Both sequences contain abundant and complementary information about the ZRFS ecosystem. For example, the lake-center sequence was suitable for pollen and chronological analysis, whereas the lake-margin sequence contained the vast majority of megafaunal, plant macrofossil, and invertebrate remains. The stratigraphic correlation of these sediment packages led to the integration of multiple biotic and environmental proxies that allowed an assessment of how high-elevation ecosystems in the Rocky Mountains responded to climate change during the late Pleistocene.

With the exception of a couple of key intervals, the ZRFS paleontological record suggests strong coupling of local climate and ecology with global climate during MIS 6/5/4 at the Marine Oxygen Isotope substage-level. The transition from MIS 6 to 5e at the site was dramatic and manifested in both significantly increased temperature and ecosystem productivity. The ZRFS record also supports the interpretation that MIS 5e was warmer than MIS 1, and that MIS 5e was as dry or drier than today. Proxy data from MIS 5c, 5a and 4 at the ZRFS show that the ecosystem responded to global climate in a way that was similar to other near-shore marine and lacustrine sites in North America. However, we stress again that the reader should not make inferences regarding leads or lags when comparing the ZRFS record with global conditions because of issues of circularity related to the three assigned ages near the top of the section.

Despite the clear manifestations of ocean–atmosphere coupling and strong hemisphere-scale teleconnections in the ZRFS record, at least two key intervals at the site showed unexpected ecological and environmental responses to changing climate conditions. First, the response at the ZRFS during MIS 5d was significantly muted compared to other North American sites and remained warm (similar to MIS 5e and 5c) despite possible continental ice growth and a decrease in global temperatures. This suggests that the climate in the Rocky Mountains may have a threshold that was not met by the changing global climate during MIS 5d. Second, the response at the ZRFS during MIS 5b was amplified and significantly colder than expected. The MIS 5c–5b transition served both to reorganize the vegetation surrounding the ZRFS to a *Picea*-dominated conifer forest with abundant graminoids and no local deciduous trees or shrubs and to shift the megafauna from that present in MIS 6 to 5c (*M. americanum*, *B. latifrons*, and *M. jeffersonii*) to that present in MIS 5a to 4 (*M. columbi* and *Bison* sp.).

The ZRFS record is unique in that it spans the penultimate glacial–interglacial–glacial sequence of the late Pleistocene, including all of MIS 5, and has stratigraphic continuity, a robust chronological framework, is located at high elevation in the Rocky Mountains, and contains an unprecedented paleontological record. Locally, it shows that high-elevation ecosystems in the Rocky Mountains of Colorado are climatically sensitive and vary significantly at the sub-millennial timescale to changing environments. Regionally, it shows that the climatic response at high elevation in the mid-latitudes of North America to global climate change had both expected and unexpected results. It also demonstrates the importance and strength of known hemisphere-scale teleconnections while underpinning the fact that regions, and possibly sub-regions at different elevations, respond differently to changing environmental pressures.

Acknowledgments

We thank the Denver Museum of Nature & Science (DMNS), President and CEO George Sparks, and the DMNS Board of Trustees for supporting the project. This project would not have been possible without the dedication and countless hours logged by DMNS staff, volunteers, and interns. Special thanks are due to the Gould and Hudick construction companies for their assistance during excavations. Similarly, the Snowmass Water and Sanitation District provided invaluable support. Preparation of specimens was conducted by the many dedicated volunteers in the DMNS Schlessman Family Earth Sciences Laboratory. The National Geographic Society, National Science Foundation, U.S. Geological Survey's Climate and Land Use Research and Development Program, and many generous private donors provided the necessary funding to support the project. A full list of all of those that contributed to the project can be found in Johnson and Miller (2012). Finally, this manuscript benefited from the constructive reviews from Marith Reheis and Harland Goldstein, both USGS (Denver). Any use of trade, product, or firm names in this website or publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yqres.2014.07.004.

References

Adam, D.P., Robinson, S.W., 1988. Palynology of two Upper Quaternary cores from Clear Lake, Lake County, California. U.S. Geological Survey Professional Paper, 1363 (86 pp.).

Adam, D.P., Sims, J.D., Throckmorton, C.K., 1981. 130,000-yr continuous pollen record from Clear Lake, Lake County, California. Geology 9, 373–377.

Anderson, R.S., Jiménez-Moreno, G., Ager, T., Porinchu, D., 2014. High-elevation paleoenvironmental change during MIS 6–4 in the central Rockies of Colorado as determined from pollen analysis. Quaternary Research 82, 542–552 (in this volume).

Baker, R.G., 1986. Sangamonian (?) and Wisconsinan paleoenvironments in Yellowstone National Park. Geological Society of America Bulletin 97, 717–736.

Balco, G., Stone, J.O., Lifton, N.A., Dunai, T.J., 2008. A complete and easily accessible means of calculating surface exposure ages or erosion rates from ^{10}Be and ^{26}Al measurements. Quaternary Geochronology 3, 174–195.

Bell, C.J., Lundelius Jr., E.L., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez Jr., D.R., Semken Jr., H.A., Webb, S.D., Zakrzewski, R.J., 2004. The Blancan, Irvingtonian, and Rancholabrean mammal ages. In: Woodburne, M.O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York, pp. 232–314.

Berger, A.L., Loutre, M.F., 1991. Insolation values for the climate of the last 10 million years. Quaternary Science Reviews 10, 297–317.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age–depth models using an autoregressive gamma process. Bayesian Analysis 6, 457–474.

Brown, P.M., Nash, S.E., Kline, D., 2014. Identification and dendrochronology of wood found at the Ziegler Reservoir fossil site, Colorado, USA. Quaternary Research 82, 575–579 (in this volume).

Bryant, B., 1972. Geologic map of the Highland Peak quadrangle, Pitkin County, Colorado, U.S. Geological Survey Map GC-932, 1:24,000 scale.

CAPE-Last Interglacial Project Members, 2006. Last Interglacial Arctic warmth confirms polar amplification of climate change. Quaternary Science Reviews 25, 1383–1400.

Coplen, T.B., Winograd, I.J., Landwehr, J.M., Riggs, A.C., 1994. 500,000-Year stable carbon isotopic record from vein calcite in Devils Hole, Nevada. Science 263, 361–365.

Cutler, K.B., Edwards, R.L., Taylor, F.W., Cheng, H., Adkins, J., Gallup, C.D., Cutler, P.M., Burr, G. S., Bloom, A.L., 2003. Rapid sea-level fall and deep-ocean temperature change since the last interglacial period. Earth and Planetary Science Letters 206, 253–271.

Elias, S.A., 2014. Environmental interpretation of fossil insect assemblages from MIS 5 at Ziegler Reservoir, Snowmass Village, Colorado. Quaternary Research 82, 592–603 (in this volume).

EPICA community members, 2004. Eight glacial cycles from an Antarctic ice core. Nature 429, 623–628.

Fawcett, P.J., Werne, J.P., Anderson, R.S., Heikoop, J.M., Brown, E.T., Berke, M.A., Smith, S., Goff, F., Hurley, L., Cisneros-Dozal, L.M., Schouten, S., Sinninghe Damsté, J.S., Huang, Y., Toney, J., Fessenden, J., WoldeGabriel, G., Atudorei, V., Geissman, J.W., Allen, C.D., 2011. Extended megadroughts in the southwestern United States during Pleistocene interglacials. Nature 470, 518–521.

Fisher, D.C., Cherney, M.D., Newton, C., Rountrey, A.N., Calamari, Z.T., Stucky, R., Lucking, C., Petrie, L., 2014. Taxonomic overview and tusk growth analyses of Ziegler Reservoir proboscideans. Quaternary Research 82, 518–532 (in this volume).

Graham, R.W., Lundelius, J.E.L., 2010. FAUNMAP II: New Data for North America with a Temporal Extension for the Blancan, Irvingtonian and Early Rancholabrean. (http://www.ucmp.berkeley.edu/faunmap/about/index.html).

Haskett, D.R., Porinchu, D.F., 2014. A quantitative midge-based reconstruction of mean July air temperature from a high-elevation site in central Colorado, USA, for MIS 6 and 5. Quaternary Research 82, 580–591 (in this volume).

Heusser, L.E., 1995. Pollen stratigraphy and paleoecologic interpretation of the 160-K.Y. record from Santa Barbara Basin, Hole 893A. In: Kennett, J.P., Baldauf, J.G., Lyle, M. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, pp. 265–277.

Heusser, L.E., 2000. Rapid oscillations in western North America vegetation and climate during oxygen isotope stage 5 inferred from pollen data from Santa Barbara Basin (Hole 893A). Palaeogeography, Palaeoclimatology, Palaeoecology 161, 407–421.

Heusser, L.E., Oppo, D., 2003. Millennial- and orbital-scale climate variability in southeastern United States and in the subtropical Atlantic during marine isotope stage 5: evidence from pollen and isotopes in ODP site 1059. Earth and Planetary Science Letters 214, 483–490.

Jiménez-Moreno, G., Anderson, R.S., 2012. Pollen and macrofossil evidence of late Pleistocene and Holocene tree line fluctuations from an alpine lake in Colorado, USA. The Holocene 23, 68–77.

Jiménez-Moreno, G., Anderson, R.S., Fawcett, P.J., 2007. Orbital- and millennial-scale vegetation and climate changes of the past 225 ka from Bear Lake, Utah-Idaho (USA). Quaternary Science Reviews 26, 1713–1724.

Jiménez-Moreno, G., Anderson, R.S., Atudorei, V., Toney, J.L., 2011. A high-resolution record of vegetation, climate, and fire regimes in the mixed conifer forest of northern Colorado (USA). Geological Society of America Bulletin 123, 240–254.

Johnson, K.R., Miller, I.M., 2012. Digging Snowmastodon: Discovering an Ice Age World in the Colorado Rockies. Denver Museum of Nature and Science and People's Press, Denver.

Kaufman, D.S., Bright, J., Dean, W.E., Rosenbaum, J.G., Moser, K., Anderson, R.S., Colman, S.M., Heil, C.W.J., Jimenez-Moreno, G., Reheis, M.C., Simmons, K.R., 2009. A quarter-million years of paleoenvironmental change at Bear Lake, Utah and Idaho. Geological Society of America Special Papers 450, 311–351.

Keigwin, L.D., Curry, W.B., Lehman, S.J., Johnson, S., 1994. The role of the deep ocean in North Atlantic climate change between 70 and 130 kyr ago. Nature 371, 323–325.

Kleman, J., Jansson, K., de Angelis, H., Stroeven, A.P., Hattestrand, C., Alm, G., Glasser, N., 2010. North American ice sheet build-up during the last glacial cycle, 115–21 kyr. Quaternary Science Reviews 29, 2036–2051.

Krell, F.T., 2014. Pleistocene dung beetles from MIS 5 at Ziegler Reservoir, Snowmass Village, Colorado (*Coleoptera*: *Scarabaeidae*: *Aphodiinae*). Denver Museum of Nature and Science Annals 5, 1–12.

Kukla, G.J., Bender, M.L., de Beaulieu, J.-L., Bond, G., Broecker, W.S., Cleveringa, P., Gavin, J.E., Herbert, T.D., Imbrie, J., Jouzel, J., Keigwin, L.D., Knudsen, K.-L., McManus, J.F., Merkt, J., Muhs, D.R., Muller, H., Poore, R.Z., Porter, S.C., Seret, G., Shackleton, N.J., Turner, C., Tzedakis, P.C., Winograd, I.J., 2002. Last interglacial climates. Quaternary Research 58, 2–13.

Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A.C.M., Levrard, B., 2004. A long term numerical solution for the insolation quantities of the Earth. Astronomy and Astrophysics 428, 261–285.

Leonard, E.A., Plummer, M.A., Carrara, P.E., 2014. Numerical modeling of the Snowmass Creek paleoglacier, Colorado, and climate in the Rocky Mountains during the Bull Lake glaciation (MIS 6). Quaternary Research 82, 533–541 (in this volume).

Licciardi, J.M., Pierce, K.L., 2008. Cosmogenic exposure age chronologies of Pinedale and Bull Lake glaciations in greater Yellowstone and the Teton Range, USA. Quaternary Science Reviews 27, 814–831.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene–Pleistocene stack of 57 globally distributed benthic δ^{18}O records. Paleoceanography 20, 1–17.

Litwin, R.J., Smoot, J.P., Pavich, M.J., Markewich, H.W., Brook, G., Durika, N.J., 2013. 100,000-year-long terrestrial record of millennial-scale linkage between eastern North America mid-latitude paleovegetation shifts and Greenland ice-core oxygen isotope trends. Quaternary Research 80, 291–315.

Loutre, M.F., Berger, A., 2003. Stage 11 as an analogue for the present interglacial. Global and Planetary Change 36, 209–217.

Lucking, C., Johnson, K.R., Pigati, J.S., Miller, I.M., 2012. Primary Mapping and Stratigraphic Data and Field Methods for the Snowmastodon Project. Denver Museum of Nature and Science, Denver, CO, p. 102.

Lyle, M., Heusser, L.E., Herbert, T., Mix, A., Barron, J., 2001. Interglacial theme and variations: 500 k.y. of orbital forcing and associated responses from the terrestrial and marine biosphere, U.S. Pacific Northwest. Geology 29, 1115–1118.

Mahan, S.A., Gray, H.J., Pigati, J.S., Wilson, J., Lifton, N.A., Paces, J.B., Blaauw, M., 2014. A geochronologic framework for the Ziegler Reservior fossil site, Snowmass Village, Colorado. Quaternary Research 82, 490–503 (in this volume).

Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore, T.C.J., Shackleton, N.J., 1987. Age dating and the orbital theory of the ice ages: development of a high-resolution 0 to 300,000-year chronostratigraphy. Quaternary Research 27, 1–29.

Miller, D.M., Miller, I.M., Jackson, S.T., 2014. Biogeography of Pleistocene conifer species from the Ziegler Reservoir fossil site, Snowmass Village, Colorado. Quaternary Research 82, 567–574 (in this volume).

Muhs, D.R., Ager, T.A., Begét, J.E., 2001. Vegetation and paleoclimate of the last interglacial Period, central Alaska. Quaternary Science Reviews 20, 41–61.

Muhs, D.R., Simmons, K.R., Steinke, B., 2002. Timing and warmth of the Last Interglacial Period: new U-series evidence from Hawaii and Bermuda and a new fossil compilation for North America. Quaternary Science Reviews 21, 1355–1383.

Peteet, D., Rind, D., Kukla, G.J., 1992. Wisconsin ice-sheet initiation: Milankovitch forcing, paleoclimatic data, and global climate modeling. Geological Society of America Special Papers 270, 53–70.

Pigati, J.S., Miller, I.M., Johnson, K.R., Honke, J.S., Carrara, P.E., Muhs, D.R., Skipp, G., Bryant, B., 2014. Geologic setting and stratigraphy of the Ziegler Reservoir fossil site, Snowmass Village, Colorado. Quaternary Research 82, 477–489 (in this volume).

Pinsof, J.D., 1996. Current status of North American Sangamonian local faunas and vertebrate taxa. In: Stewart, K.M., Seymour, K.L. (Eds.), Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals. University of Toronto Press, Toronto, pp. 156–190.

Pinsof, J.D., 1997. A Late Pleistocene Sangamonian vertebrate fauna from eastern Texas. Texas Journal of Science 491, 3–22.

Pisias, N.G., Mix, A.C., Heusser, L.E., 2001. Millennial scale climate variability of the northweast Pacific Ocean and northwest North America based on radiolaria and pollen. Quaternary Science Reviews 20, 1561–1567.

Reheis, M.C., Bright, J., Lund, S.P., Miller, D.M., Skipp, G., Fleck, R.J., 2012. A half-million-year record of paleoclimate from the Lake Manix core, Mojave Desert, California. Palaeogeography, Palaeoclimatology, Palaeoecology 365–366, 11–37.

Rohling, E.J., Braun, K., Grant, K., Kucera, M., Roberts, A.P., Siddall, M., Trommer, G., 2010. Comparison between Holocene and marine isotope stage-11 sea-level histories. Earth and Planetary Science Letters 291, 97–105.

Sánchez Goñi, M.F., Eynaud, F., Shackleton, N.J., 1999. High resolution palynological record off the Iberian margin: direct land–sea correlation of the Last Interglacial complex. Earth and Planetary Science Letters 171, 123–137.

Scherer, R.P., Bohaty, S.M., Dunbar, R.B., Esper, O., Flores, J.-A., Gersonde, R., Harwood, D.M., Roberts, A.P., Taviani, M., 2008. Antarctic records of precession-paced insolation-driven warming during early Pleistocene marine isotope stage 31. Geophysical Research Letters 35 (L03505).

Scott, W.E., Pierce, K.L., Bradbury, J.P., Forester, R.M., 1982. Revised Quaternary stratigraphy and chronology in the American Falls area, southeastern Idaho. In: Bonnichsen, B., Breckenridge, R.M. (Eds.), Cenozoic Geology of Idaho. Idaho Bureau of Mines and Geology Bulletin, Moscow, ID, pp. 581–595.

Sertich, J.J.W., Stucky, R., McDonald, H.G., Newton, C., Fisher, D.C., Scott, E., Demboski, J.R., Lucking, C., McHorse, B.K., Davis, E.B., 2014. High-elevation late Pleistocene (MIS 6–5) vertebrate faunas from the Ziegler Reservoir fossil site, Snowmass Village, Colorado. Quaternary Research 82, 504–517 (in this volume).

Sharpe, S.E., Bright, J., 2014. A high-elevation MIS 5 hydrologic record using mollusks and ostracodes from Snowmass Village, Colorado, USA. Quaternary Research 82, 604–617 (in this volume).

Strickland, L.E., Baker, R.G., Thompson, R.S., Miller, D.M., 2014. Last interglacial plant macrofossils and climates from Ziegler Reservoir, Snowmass Village, Colorado, USA. Quaternary Research 82, 553–566 (in this volume).

Tzedakis, P.C., 2010. The MIS 11–MIS 1 analogy, southern European vegetation, atmospheric methane and the "early anthropogenic hypothesis". Climate of the Past 6, 131–144.

Whitlock, C., Bartlein, P.J., 1997. Vegetation and climate change in northwest America during the past 125 kyr. Nature 388, 57–61.

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog plant communities, and ecological surprises: past and future. Frontiers in Ecology and the Environment 5, 475–482.

Williams, J.W., Shuman, B.N., Webb III, T., Bartlein, P.J., Leduc, P.L., 2004. Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. Ecological Monographs 74, 309–334.

Winograd, I.J., Coplen, T.B., Landwehr, J.M., Riggs, A.C., Ludwig, K.R., Szabo, B.J., Kolesar, P.T., Revesz, K.M., 1992. Continuous 500,000-year climate record from vein calcite in Devils Hole, Nevada. Science 258, 255–260.

Woolfenden, W.B.A., 2003. 180,000-Year record from Owens Lake, CA: terrestrial vegetation change on orbital scales. Quaternary Research 59, 430–444.