Holocene hydroclimate and environmental change inferred from a high-resolution multi-proxy record from Lago Ditkebi, Chirripó National Park, Costa Rica

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ARTICLE INFO

Keywords:
Abrupt climate change
5200 cal yr BP event
Chironomids
Fire history
Sediment geochemistry
Charcoal

ABSTRACT

Multi-proxy analysis of a sediment core recovered from Lago Ditkebi in Chirripó National Park, Costa Rica, was undertaken to develop a multi-decadal to sub-centennial-scale reconstruction of Holocene hydroclimate and environmental change for the region. Analyses of sub-fossil chironomid assemblages, macroscopic charcoal, and bulk sediment geochemistry suggest that the glacial highlands in Chirripó National Park experienced notable hydroclimate variability, periodical burning by wildfires and climate-related vegetation change during the last ~8100 years. A single chironomid taxon, Procladius, most commonly associated with cold glacial lakes in Costa Rica, dominates the Holocene sub-fossil chironomid assemblage in Lago Ditkebi. Inferred from the proxy records, the interval between ~8100 and 5270 cal yr BP at the glacial highlands was relatively cold and dry with low effective moisture and limited fire activity. Cool and dry conditions were also observed between ~2820 cal yr BP and present but co-occurred with more frequent, low-severity fires. The highest fire frequency occurred between ~3300 and 1600 cal yr BP. The shifts in the chironomid assemblage and the low δ13C values detected between ~5270 and 2820 cal yr BP suggest a warm and wet climate and a decrease in abundance of Muhlenbergia, a C4 grass during that time. Concurrent maxima in C/N, charcoal accumulation and the abundance of thermophilous chironomid taxon, Polypedilum N type, at ~5200 cal yr BP are indicative of an abrupt climate change event that was characterized by rapid warming, quickly increased effective moisture and intense wildfires in the glacial highlands of Costa Rica.

1. Introduction

The vulnerability of high-elevation regions, such as the Cordillera de Talamanca in Costa Rica, to global climate change is extremely high, due in part to vertical amplification of warming (Beniston and Haeberli, 2000; Karmalkar et al., 2011; Pepin et al., 2015). Developing a long-term perspective of climate variability for Central America broadly, and Costa Rica more specifically, through paleoclimate and paleoenvironmental studies, can help understand the mechanisms driving hydroclimate variability and climate change in the Neotropics (tropical Americas). Our understanding of late Quaternary paleoclimate and paleoenvironmental change in the Neotropics remains relatively limited in comparison to the mid- and high latitude regions of the northern hemisphere. Recent paleoenvironmental reconstructions have demonstrated that significant fluctuations in precipitation (amount and intensity) and sea surface temperatures (SSTs) characterized the late Quaternary in the Neotropics and adjacent oceans (e.g. Horn, 2007). This has led to the rejection of the earlier assumption of tropical climate stability during the late Quaternary (CLIMAP Project Members, 1981, 1984; Thompson et al., 1997; Bundschuh and Alvarado, 2007; Horn, 2007). In addition, multiple lines of evidence indicate that the Holocene itself was a time of considerable climatic variability in the tropical Americas (Mayle et al., 2000; Peterson et al., 2000; Haug et al., 2001; Hodell et al., 2005a, 2005b; Horn, 2007; Lachniet et al., 2012). However, to-date, the availability of high-resolution paleoclimate and paleoenvironmental reconstructions, particularly thermal reconstructions, remain limited for the Neotropics.

Chironomids (Insecta: Diptera: Chironomidae) are the most abundant insects found in freshwater ecosystems (Cranston, 1995) and are sensitive to air and water temperature change (Eggermont and Heiri, 2012). The application of chironomid-air temperature inference models to the sub-fossil chironomid assemblages extracted from late...
Quaternary lacustrine sediment cores have provided reliable estimates of long-term thermal conditions for many regions (see references cited in Porinchu and MacDonald, 2003; Walker and Cwynar, 2006; Eggertmont and Heiri, 2012). The existence of a strong correlation between mean annual air temperature (MAAT) and modern distribution of chironomids in Costa Rican lakes enabled the establishment of chironomid-based inference model for MAAT (Wu et al., 2015). Application of this inference model to the upper 2.90 m of sediment core extracted from Laguna Zoncho in southern Costa Rica, facilitated the development of a ~3200-year record of thermal variability at a centennial-scale. This record indicated that the late Holocene in Costa Rica was characterized by remarkable thermal variability and provided support for regional expression of the Medieval Climate Anomaly and the Little Ice Age (Wu et al., 2017). However, limited temporal resolution prevented the development of a more highly resolved record of hydro-climate and paleoenvironmental change for this region and the length of the core restricted the record to the late Holocene. Here we make use of an existing chironomid-based calibration set from Costa Rica (Wu et al., 2015), together with geochemistry and charcoal analyses of a 5.75 m sediment core recovered from Lago Ditkebi, a glacial lake in Chirripó N.P., Costa Rica, to reconstruct hydroclimate variability and paleoenvironmental change in southern Central America during the Holocene. This study aims to: 1) develop a high-resolution (multi-decadal to sub-centennial scale) reconstruction of Holocene thermal variability, 2) characterize paleoenvironmental change, including fire regime and vegetation dynamics through the Holocene, and 3) determine if evidence for abrupt climate change events, e.g. the 5200 cal yr BP event, are recorded at Lago Ditkebi.

2. Study site

Lago Ditkebi (9°28′06″ N, 83°28′49″W; 3520 m.a.s.l.; Esquivel-Hernández et al., 2018) is located on the east of the crest of the Cordillera de Talamanca on the Atlantic slope in Chirripó N.P., in Costa Rica (Fig. 1A). It is a permanent, natural lake, formed by glacial activity during the late Quaternary and underlain by pyroclastic deposits (Haberyan et al., 2003; Horn et al., 2005). It is characterized by extremely dilute (specific conductivity = 0.029 S/cm), slightly alkaline (pH = 8) water. The lake, which is moderately deep (depth = ~8 m; Fig. 1B), has a relatively uniform temperature profile that surface temperature of 10.7°C gradually decreases to 10.3°C at 4 m and stay constant downward. Lago Ditkebi is surrounded by páramo, an alpine ecosystem composed of a diverse mixture of evergreen shrubs, grasses, and perennial herbaceous plant assemblages of Andean origin (Kappelle and Horn, 2016). The herbaceous cover at the site is dominated by dwarf bamboo (Chusquea subtessellata), sedges and grasses, including Muhlenbergia, a C4 grass widely found in Chirripó N.P. (Horn, 1990; Lane et al., 2011). Precipitation records from the Cerro Páramo meteorological station (3466 m a.s.l., ~30 km west of the study site; Horn, 1993) show distinct wet and dry seasons, which results from the annual migration of Intertropical Convergence Zone (ITCZ), with ~90% of the precipitation falling between May and November (Horn et al., 2005). High atmospheric humidity moderates the dry season, but intervals of cloud-free weather associated with the northeast (NE) trade wind inversion lowers humidity sufficiently enough to support fires (Horn and Kappelle, 2009).

Fires have occurred throughout the 20th century in the park, and the causes of fires are complex. Many of the recent fires (1953, 1958, 1976, 1977, 1981, 1992) affecting the Chirripó páramo appear to be human-initiated (Horn and Kappelle, 2009). Climatic factors have also played an important role. Large fires have been documented during the driest months (February, March, < 0.5 mm precipitation) in 1961, 1976 and 1985 in the Chirripó páramo and the adjacent montane forests (Horn and Kappelle, 2009). Thunderstorm-induced lightning, which has been observed striking the high elevations of the park (Horn and Kappelle, 2009), has ignited at least one forest fire (Chavert-Polini and Esquivel-Garrote, 2005). Pre-historic fires in the páramo of Chirripó N.P. were most likely ignited by lightning (Horn and Kappelle, 2009).

3. Methods

A 5.75 m sediment core was recovered from the center of Lago Ditkebi (DKB) at a depth of 8.0 m in July 2014. The upper 0.84 m of sediment was recovered using a plastic tube fitted to a modified Livingstone corer, with the remainder of the sediment recovered using a stainless-steel barrel. The Livingstone corer was deployed from a platform established on two inflatable rafts. The upper 0.84 m of the sediment core was sub-sectioned in the field at 0.25 cm intervals and stored in Whirl-Paks. The remainder of the lake sediment core was cut into ~50 cm sections, wrapped with plastic film and aluminum foil, encased in PVC tubes for transport to the United States, and later sectioned at 0.50 cm intervals in the Environmental Change Lab at the University of Georgia. The stratigraphy of the DKB core was well preserved but a depth adjustment was applied following sectioning accounting for core compression by multiplying the ratio of core length measured in the field versus in the lab. For example, the core drive DKB-14-LC1Ea (275–345 cm) was 70 cm in the field, but it was determined to be 66 cm in the lab, due to water evaporation during the transportation. Thus, all the sample depths for this section of the core were adjusted using a multiplier of 1.061 (70/66) when the core was sectioned at 0.5 cm interval in the lab.

Chronological control for DKB core is based on eight AMS radiocarbon (14C) dates obtained on charcoal and aquatic moss (Table 1). Radiocarbon dates were converted to calendar years using the most recent IntCal13 calibration curve (CALIB 7.10: calib.org/calib.html; Reimer et al., 2013) with the full set of calibrated ± 2σ ages reported. An age-depth model (Fig. 2), constructed based on a probabilistic sampling method implemented using Clam 2.2, provided a reasonable sedimentation rate and deposition curve (setting: smooth-spline type = 4, smooth level = 0.3; Blauuw, 2010). All ages are reported in CE or cal yr BP relative to 1950 CE. The lowest radiocarbon date in the DKB core, obtained at 539 cm, provides a date of 6150 14C yr BP ± 20 years. An extrapolation of the age-depth model generates a modeled estimate of the basal age of the core as ~8100 cal yr BP. Radiocarbon dating was conducted at the Center for Applied Isotope Studies (CAIS) at the University of Georgia.

Analysis of sub-fossil chironomid remains followed the procedures outlined in Walker (2001). A total of 98 sediment samples were analyzed for sub-fossil chironomid remains at a sub-centennial scale resolution (~90 years/sample). A known volume of sediment (3–5 ml) was placed in a beaker with 50 ml of 5% KOH and heated at 50°C for ~30 min to facilitate the break-up of colloidal matter. The deflocculated sediment was washed through a 95 µm mesh and rinsed using distilled water. The material retained on the mesh was back-washed into a beaker. Samples were poured into a Bogorov plankton counting tray and the chironomid head capsules were isolated from the sediment matrix using a dissection microscope at 50 × magnification. The chironomid head capsules were permanently mounted on slides in Entellan® for identification. A minimum of fifty chironomid head capsules were identified in each sample (Heiri and Lotter, 2001). Taxonomic identification was conducted at 400 ×, to genus, relying primarily on Wu et al. (2015) and larval keys for Florida and North and South Carolina (Epler, 1995, 2001), with Brooks et al. (2007), Cranston (2010), Eggermont et al. (2008) and Spies et al. (2009) for additional diagnostic information. Chironomid percentage diagrams were plotted using C2 (Juggins, 2003). Numeric analyses were based on the relative abundance of all identifiable chironomid remains. Due to the dominance of Procladius throughout the core, the zonation of the chironomid diagram is based on visually observed changes in the relative abundance of a key chironomid taxon, Polypedilum N type, which was quantified using Z scores (mean = 0.60, standard deviation = 0.97).
Additionally, rarefaction analysis was implemented to assess variations in taxon richness (Birks and Line, 1992). Faunal turnover was assessed using detrended canonical correspondence analysis (DCCA) (Zuur et al., 2007) in CANOCO version 4.0 (Ter Braak and Smilauer, 1998), using the square-root transformed chironomid percentage data to optimize the ‘signal’ to ‘noise’ ratio and to stabilize variance (Prentice, 1980).

Macroscopic charcoal was analyzed using the protocol available from the Limnological Research Center at the University of Minnesota (http://lrc.geo.umn.edu/laccore/procedures.html). Charcoal analysis for the Lago Ditkebi core was based on 367 sediment samples, consisting of 1.5—2 cm³ of material. The sediment was sampled contiguously at 1 cm intervals between the surface and 84 cm, at 1.1—1.2 cm intervals between 84 cm and 138 cm, at 1.6—2.5 cm interval between 138 and 373.9 cm, at 2 cm intervals between 374 and 453 cm, at 1.1—1.2 cm intervals between 453 and 485 cm and 2 cm intervals between 485 and 575 cm. Sampling intervals reflect the adjusted depths. Sediment samples were washed into beakers using distilled water, followed by a treatment of 30 ml solution of 6% hydrogen peroxide (H₂O₂) to bleach the organic matter. Beakers were covered by aluminum foil to avoid contamination and placed into a drying oven and heated at 50 °C for ~24 h to amplify the bleaching reaction. Samples were washed through nested sieves of 125 μm and 250 μm mesh size, the material remaining on the sieves were transferred into labeled petri dishes. To disperse the charcoal and make counting and identification easier, ~2 ml of a detergent solution (dilute [0.5%] sodium hexametaphosphate) was added to each petri dish. After the water in the petri dishes evaporated, charcoal fragments were tallied using a gridded counting sheet at 100 × magnification and classified as either woody, grass, or lattice-type, providing additional information on fuel type. Woody charcoal, produced by trees and shrubs, can be identified by its sheen as well as thick, layered and prismatic structure. Charcoal derived from grass is usually thin, flat, and characterized by stomata in the epidermal walls (Walsh et al., 2008, 2014 and Walsh et al., 2010). Charcoal produced by the burning of thin leaves is characterized by a flat, single-layered, lattice pattern (Jensen et al., 2007; Walsh et al., 2008, 2014 and Walsh et al., 2010). Analysis and interpretation of the charcoal is limited to the > 125 μm fraction because charcoal belonging to this size typically reflects the occurrence of a local fire (Whitlock and Millspaugh, 1996; Walsh et al., 2008). Charcoal counts were divided by the volume of the sample to calculate charcoal concentration (particles/cm³). We followed the methods outlined in Higuera (2009) and used the statistical program CharAnalysis (Higuera, 2009; http://charanalysis.googlepages.com/) to analyze the charcoal data. The interpolation window, used to calculate the non-log-transformed charcoal accumulation rate (CHAR), was set at fifteen years, and determined by the median sampling resolution (17 years) of all raw samples. A LOWESS smooth (robust to outliers) with a 500-year window was applied to the charcoal records used for estimating background CHAR.
(C_{background}) to ensure > 30 interpolated samples in the analysis window. Because of the notable variability in C_{background} observed through the record, the threshold value of fire peak was defined locally to separate fire-induced (i.e. signal) from non-fire related variability (i.e. noise) in the high-frequency CHAR component (C_{peak}). Residuals (C_{peak} = C_{interpolated} − C_{background}) were calculated for C_{peak}. Under this setting, the final positive CHAR threshold (threshFinalPos) was selected and determined the cut-off for individual fire peaks. The total number of fire peaks is based on the results of peaksFinal.

### Geochemical Analyses

Geochemical analyses of the lake sediment recovered from Lago Ditkebi included total organic carbon (C%), total organic nitrogen (N%) and the stable isotope of carbon (δ^{13}C). The geochemical analyses were based on 146 samples that were freeze-dried for 24 to 72 h. Approximately 3—4 mg of sediment for each sample was weighed out on a high-precision digital scale and placed in silver capsules. These samples were pretreated, prior to being combusted, with 10—50 μL of distilled hydrochloric acid (5% HCl) using a pipet to remove any carbonates. The sediment samples were not milled following freeze-drying due to the fine-grained nature of the sediment. For the few samples that contained coarser-grained sediment, three replicate samples were measured and the average value of geochemical data was calculated to ensure the representativeness of the results. All geochemical analyses were conducted at the Center for Applied Isotope Studies (CAIS) at the University of Georgia.

### Table 1

<table>
<thead>
<tr>
<th>Core code</th>
<th>Lab code</th>
<th>Depth in core (cm)</th>
<th>Material</th>
<th>Uncalibrated 14C age (14C yr BP)</th>
<th>Standard error (±)</th>
<th>2σ Age range</th>
<th>Relative area under distribution</th>
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<td>Charcoal</td>
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<td>20</td>
<td>1422-1451 CE</td>
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<tr>
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<td>112.5-113.0</td>
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<td>20</td>
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<td>150.5-151.0</td>
<td>Charcoal</td>
<td>6150</td>
<td>20</td>
<td>1422-1451 CE</td>
<td>0.994</td>
</tr>
</tbody>
</table>

Fig. 2. Age-depth model for Lago Ditkebi. The calibration probability of individual dates are indicated in blue with the gray band depicting the 95% probability intervals for the modeled ages established using Clam (http://www.chrono.qub.ac.uk/blaauw/clam.html, Blaauw, 2010). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Fig. 3. Relative abundance diagram for the sub-fossil chironomids from Lake Ditkebi. Chironomid taxa have been arranged according to their MAAT optima (Wu et al., 2015), with temperature optima increasing from left to right. Taxa with MAAT optima < 19 °C, or reported as common constituents of high-elevation lakes (Wu et al., 2015; Spies et al., 2009) are colored in blue. Taxa with MAAT optima > 20 °C, or associated with low-elevation lakes (Wu et al., 2015) are colored in orange. *Chironomus*, a taxon with an MAAT optimum of 19.2 °C (Wu et al., 2015), which is most abundant in mid-elevation lakes, is colored in green. Taxa with no specific habitat preference or unknown MAAT optima are plotted in black. Taxa with names underlined are not observed in modern training set (Wu et al., 2015). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Fig. 4. Charcoal concentration, sedimentation rate, charcoal accumulation rate (CHAR) and CharAnalysis results (Higuera, 2009) for Lago Ditkebi. Charcoal concentration is calculated for each of the morphotypes. CHAR is based on the sum of all charcoal morphotypes (> 125 μm). Chironomid assemblage-based zones are also indicated.
4. Results

4.1. Chironomids

A total of eighteen chironomid taxa were present in the DKB core (Fig. 3), fifteen of which (83%) are present in the modern training set (Wu et al., 2015). Three taxa, Diamesa, Corynocera, and Parochlus, are not found in the modern training set in Wu et al. (2015); but Corynocera and Parochlus have been reported in taxonomic survey of Costa Rica in Spies et al. (2009). The relative abundance of Procladius, which dominates the chironomid assemblage throughout the entire core, varies between 84% and 100%. Psectrocladius is the second most abundant taxon at Lago Ditkebi, however, its relative abundance never exceeds 15%. Seven taxa, Unknown ii, Smittia/Pseudosmittia, Corynoneura/Thienemanniella, Polypedilum N type, Cricotopus/Orthocladius, Parochlus and Synorhocladius, are also present in DKB core, albeit at relatively low levels, with the maximum relative abundance of these taxa < 6% of the total identifiable chironomid remains in any given sample. Eleven of the eighteen chironomid taxa present in Lago Ditkebi during the Holocene are associated with cold, high-elevation lakes (highlighted in blue in Fig. 3) in the modern training set (Wu et al., 2015). Because of the dominance of Procladius and other cold climate indicators, we make zonation be based on the change in Z-scores of the relative abundance of Polypedilum N type, a warm climate indicator (Wu et al., 2015) with relatively high values in the relative abundance and frequency of occurrence in the core (highlighted in orange in Fig. 3). The frequent presence of Polypedilum N type and its pronounced high Z-scores above the mean between ~5270 and 2820 cal yr BP were used as key references to demarcate zone DKB-II. The intervals from 8100 to 5270 cal yr BP and from 2820 to 2300 cal yr BP represent zones DKB-I and DKB-III, respectively. The number of head capsule remains identified varied between 50 and 162 per sample (average = 75.8 heads/sample). Rarefied taxon richness varies from 1 to 6.7, with maximum richness occurring at ~3190 cal yr BP (Fig. 3). Rarefied taxon richness begins to notably decrease at ~2800 cal yr BP, near the base of zone DKB-I.

The chironomid assemblage in zone DKB-I (8100—5270 cal yr BP), which is dominated by Procladius, also includes Psectrocladius, Cricotopus/Orthocladius, Parochlus and Synorhocladius, with much lesser amounts of Limnophyes, Unknown ii, Smittia/Pseudosmittia, Corynoneura/Thienemanniella and other cold climate indicators (Vu et al., 2015) with relatively high values in the relative abundance and frequency of occurrence in the core (highlighted in orange in Fig. 3). The frequent presence of Polypedilum N type and its pronounced high Z-scores above the mean between ~5270 and 2820 cal yr BP were used as key references to demarcate zone DKB-II. The intervals from 8100 to 5270 cal yr BP and from 2820 to 2300 cal yr BP represent zones DKB-I and DKB-III, respectively. The number of head capsule remains identified varied between 50 and 162 per sample (average = 75.8 heads/sample). Rarefied taxon richness varies from 1 to 6.7, with maximum richness occurring at ~3190 cal yr BP (Fig. 3). Rarefied taxon richness begins to notably decrease at ~2800 cal yr BP, near the base of zone DKB-I.

Zone DKB-I (8100—5270 cal yr BP), which is dominated by Procladius, also includes Psectrocladius, Cricotopus/Orthocladius, Parochlus and Synorhocladius, which is characterized by a sudden increase in the relative abundance of Polypedilum N type. The abundance of Polypedilum N type is relatively low, averaging ~1.8% through this zone, with a maximum abundance (4.4%, 4 heads/sample) occurring at ~6480 cal yr BP. Variation in chironomid assemblage concentration (54.2 head capsules/ml) occurs at ~6710. Rarefied taxon richness is generally high with average of 4.3. The DCCA scores and Z-scores of the relative abundance of Polypedilum N type stay minimal variation in this zone.

Procladius continues to dominate in zone DKB-II (5270—2820 cal yr BP). Most obviously, this zone is characterized by a sudden increase in the relative abundance of Polypedilum N type. The abundance of Polypedilum N type is relatively low, averaging ~1.8% through this zone, with a maximum abundance (4.4%, 4 heads/sample) occurring at ~5270 cal yr BP. Taxa present in zone DKB-I, including Psectrocladius, Cricotopus/Orthocladius, Parochlus, Synorhocladius, Unknown ii, Smittia/Pseudosmittia, and Corynoneura/Thienemanniella, remain extant in zone DKB-II. Smittia/Pseudosmittia and Limnophyes, taxa associated with terrestrial or semi-terrestrial conditions, are found near the onset and the termination of the zone. Zone DKB-II is also characterized by the appearance of Diamesa. Head capsule concentrations are relatively stable with average of 22.8 heads/ml. Average of rarefied taxon richness decreases slightly to 3.9 in DKB-II with much greater varied values between ~4200 and 3300 cal yr BP. DCCA scores stay lightly change in this zone. Significant variation is observed in Z-scores of the relative abundance of Polypedilum N type during DKB-II showing significant deviation from the mean.

Zone DKB-III (2820 cal yr BP—present) is still dominated by Procladius, which comprises nearly the entire chironomid assemblage in every sample in this zone. This shift is reflected by the decrease in the thermophilous taxon, Polypedilum N type, and the synchronous increase in the abundance of Chironomus, Corynocera, Microspectra and Tanytarsus LU type. This interval is followed by a reduction in Polypedilum N type, Cricotopus/Orthocladius, Parochlus and Synorhocladius with relatively muted faunal turnover and notably reduced rarefied taxon richness (average = 2.5) observed through the reminder of zone DKB-III. The interval between ~2600 and 2400 cal yr BP is characterized by a notable shift in the chironomid assemblage, as evidenced by the DCCA scores. Z-scores of the relative abundance of Polypedilum N type returns to the status of limited variation.

4.2. Charcoal analysis and sedimentation rate

Similar trends in woody and grass charcoal concentrations are observed throughout the Holocene (Fig. 4). Woody and grass charcoal concentrations are low in zone DKB-I, with slightly high charcoal concentrations observed at ~7100, 6500 and 6000 cal yr BP. Charcoal concentrations of woody and grass morphotypes rapidly increase at the base of zone DKB-II and reaches their maxima at ~5250 cal yr BP. A 1.5 cm-thick layer of large-size charcoal particles (length and width: 3000—5000 μm) observed at 471.5—473 cm in the sediment core corresponds to the high concentration of woody and grass charcoal occurred at this time. Elevated charcoal concentrations (in all morphotypes > 125 μm) also occur in zone DKB-II at ~4900, ~4400 cal yr BP and between 3200 and 2820 cal yr BP. The concentration of the lattice morphotype peaks (10 particles/cm 2) at ~4400 cal yr BP in zone DKB-II. The modeled sedimentation rate remains nearly unchanged in zone DKB-I but increases after ~5250 cal yr BP, reaching a peak at ~3250 cal yr BP (0.123 cm/yr). It gradually declines through the remainder of the DKB-III zone until the 19th century when it begins to rise.

The charcoal accumulation rate (CHAR) calculated using CharAnalysis (Higuera, 2009) based on the concentration sum of all morphotypes (> 125 μm) ranges between 0 and ~77.22 particles/cm 2/yr. CHAR increases abruptly at the onset of zone DKB-II, reaching a core maximum at this time. CharAnalysis programs identifies the occurrence of 31 discrete fire peaks during the past ~8100 years within Lago Ditkebi catchment. Three of the 31 fire peaks occur in zone DKB-I (8100—5270 cal yr BP), with more than half of the fire events (21/31; 67.7%) occurring during the interval between ~3300 cal yr BP and present. The frequency of fire peaks in DKB-I is relatively low, with one fire peak occurring every 1000 years. Zone DKB-III (2820 cal yr BP—present) is characterized by a much higher fire peak frequency, ranging from 2.13 to 5.23 peaks/ka (mean = 3.55 peaks/ka), relative to that of zones DKB-I and DKB-II. The interval with the highest fire frequency value (mean = 4.97 peaks/ka) throughout the core occurred between ~2480 and 2060 cal yr BP. Fire peak magnitude, providing reference for fire severity or proximity, show two high values of CHAR at ~5290 (2754.36 particles/cm 2/peak) and 3080 (2020.69.0 particles/cm 2/peak) cal yr BP. Three additional peaks with slightly lower values of fire peak magnitude (i.e. 801.76, 864.49 and 1096.61 particles/cm 2/peak) are observed at ~4460, ~4960 and ~1370 cal yr BP, respectively.

4.3. Geochemistry

The Lago Ditkebi sediment core is characterized by an increasing trend of N% and C% through the Holocene (Fig. 5). The C% increases from 9.3% at the base of the core to 27.6% in the most recently deposited sediment. The N% increases approximately three-fold, from 0.7% at ~8100 cal yr BP to 2.3% at present. DKB-I (~5270—2820 cal yr BP) is characterized by relatively low δ13C values (average = −25.8‰) compared to the later portion of DKB-I (Fig. 6; DKB-Ib: ~7500—5270 cal yr BP, average = −25.0‰) and zone DKB-III (average = −24.4‰). The δ13C values of DKB-II are close to that of the early interval of DKB-I (Fig. 6; DKB-Ia: ~8100—7500 cal yr BP,
average = −26.5‰). A pronounced trend of increasing δ\(^{13}\)C occurs beginning at ~2100 cal yr BP, with a δ\(^{13}\)C maximum of −21.8‰ observed at ~590 cal yr BP. The C/N value remains relatively unchanged for the entire core, with exceptions of notable, abrupt shifts at ~7170 and ~5270 cal yr BP, and relatively minor fluctuations at 6580, 5000, 4610, 4140 and 2170 cal yr BP. The shift in C/N at ~5270 cal yr BP, which is characterized by a sharp increase from 12 to 20.

5. Discussion

5.1. Chironomid paleoecology

The extremely high relative abundance of *Procladius* (minimum abundance > 84% of identifiable chironomid remains per sample) precludes the application of the chironomid-based temperature inference model in Wu et al. (2015) to the sub-fossil chironomid stratigraphy developed for Lago Ditkebi. The applicability of the existing chironomid-temperature relationship developed in Wu et al. (2015) was assessed by determining the similarity of the sub-fossil chironomid assemblages from Lago Ditkebi to their closest modern analogues. This analysis indicated that the training set did not have sufficient number of “good” analogues and that the squared residual distance between the calibration set samples and the Lago Ditkebi samples were a poor fit with temperature (Birks et al., 1990). As a result, we interpret chironomid paleoecology qualitatively and more focus on the low-count taxa. Attention should be taken that increasing the number of head capsules picked in each sample could enhance the representative of the low-count taxa.

The chironomid assemblage preserved in Lago Ditkebi is dominated by taxa indicative of cold conditions (Wu et al., 2015), with eleven of the eighteen taxa associated with cold, high-elevation lakes in the modern training set (colored blue in Fig. 3). *Procladius*, a taxon tolerant of low-oxygen (Brooks et al., 2007; Spies et al., 2009) with a mean annual air temperature (MAAT) optimum of 14.9 °C (Wu et al., 2015), dominates the chironomid community at Lago Ditkebi for the entire Holocene. The low MAAT at the site, which is a function of its elevation (~3500 m a.s.l.), and the depth of the lake, at 8 m, provide an ideal habitat for *Procladius*. *Psectrocladius*, observed consistently throughout the core, is identified as a taxon favoring the lowest temperature optimum (10.4 °C) in the modern training set (Wu et al., 2015). This taxon, in general level, is known to inhabit the littoral zone and is often associated with macrophytes (Brooks et al., 2007). *Cricotopus/Orthocladius, Synorthocladius* and *Parochlus*, observed in DKB-I and DKB-II, reflect cold conditions as well. The modern distribution of *Cricotopus/Orthocladius* and *Synorthocladius* in Costa Rica is restricted to lakes located above 3450 m a.s.l., including Lago Chirripó and Lago Morrenas, where MAAT is < 7.9 °C (Wu et al., 2015). *Parochlus* adults have been found at high-elevation volcanic sites in Costa Rica (Watson and Heyn, 1992), and the larvae in alpine streams or springs or mosses in small water bodies (Spies et al., 2009). Five additional taxa, *Limnophyes*, Unknown ii, *Smittia/Pseudosmittia*, *Corynoneura/Thienemanniella* and *Micropsectra contracta* type present in the DKB core, at relatively low abundance, are also associated with low temperatures (Wu et al., 2015), with *Limnophyes* and *Smittia/Pseudosmittia* often associated with semi-terrestrial habitats (e.g. Brooks et al., 2007).

Shifts in the composition of the sub-fossil chironomid assemblages are used to infer variations in thermal conditions during the Holocene at Lago Ditkebi (Fig. 6A–E). Z-score reflecting the temporal variation in the relative abundance of *Polypedilum N* type indicates that a distinctive change is detected in the abundance of this taxon in zone DKB-II, with little change observed in DKB-I and DKB-III (Fig. 6A). The continuous presence and high relative abundance of *Polypedilum N* type in DKB-II (~5270—2820 cal yr BP) could suggest elevated MAATs during this interval. Today in Costa Rica, *Polypedilum N* type, which has an MAAT
optimum of 22°C, is most abundant in warm, low-elevation lakes (Wu et al., 2015). The low percentage of *Polypedilum* N type in zone DKB-I and zone DKB-III is inferred to reflect the existence of similar thermal conditions that was relatively cold between 8100 and 5270 cal yr BP and between 2820 cal yr BP and present. The co-occurrence of *Diamesa* and *Polypedilum* N type in zone DKB-II is notable (Fig. 6B,C). Larvae of *Diamesa* are considered as cold stenotherms, with approximately 100 species of *Diamesa* found in the Holarctic and much fewer number of species found in the Afrotropical region (Hansen and Cook, 1976; Willassen and Cranston, 1986; Ward, 1994; Brooks et al., 2007; Cranston, 2010). The larvae of *Diamesa*, a winter active taxon that generally requires cold water, are typically limited to extremely low-temperature habitats (Bouchard Jr and Ferrington Jr, 2009; Anderson, 2012). This is the first confirmed report of this cold-adapted taxon in Costa Rica (Waston and Heyn, 1992; Brooks et al., 2007; Spies et al., 2009; Cranston, 2010; Kranzfelder, 2012; Wu et al., 2015). The presence of *Diamesa* in zone DKB-II, albeit at low relative abundance (maximum at 3.57%), likely reflects the occurrence of a persistent pool of cold bottom water at Lago Ditkebi during this interval. Lago Ditkebi is characterized by a deep central basin and a broad, shallow shelf along its southeastern margin (Fig. 1B). The temperature profile of Lago Ditkebi suggests that, even in the presence of strong NE trade winds, the lake maintains weak stratification between June and October when average daily sunlight is 2.9 hours (Coen, 1983). Pronounced stratification would be expected between November and May when the average daily duration of sunlight is 4.5 hours (Coen, 1983). During the wet season (May–October), increased rainfall would lead to an increase in lake level and the shallow shelf located along the southeastern margin of Lago Ditkebi would be inundated. This would likely result in the development of a layer of warm water at the surface of the lake. Expansion of littoral habitat associated with an increase rainfall and the deepening of the lake could facilitate an increase in the relative abundance of *Polypedilum* N type (Fig. 6B) and terrestrial/semi-terrestrial taxa (at the onset and termination of DKB-II, Fig. 6D,E), and also result in stratification and the development of a pool of cold bottom water preferred by *Diamesa* (Fig. 6C).
5.2. Holocene paleoenvironmental change

Variations in δ¹³C in the DKB core offer insight into Holocene hydroclimate and paleoenvironmental change in the region. The sensitivity of δ¹³C to shifts in the relative abundance of C₃ and C₄ plants has been used to reconstruct vegetation dynamics during the Holocene (e.g. Meyers and Lalier-Vergès, 1999; Meyers and Teranes, 2002; Meyers, 2003; Leng and Marshall, 2004; Lane et al., 2011). C₄ plants have much higher efficiency of absorbing CO₂ containing ¹³C during photosynthesis than C₃ plants do (Meyers and Teranes, 2002). When C₄ plants increase in abundance in a catchment, soil organic matter becomes more enriched in ¹³C and this signal can be archived by lake sediment when terrestrial organic matter is transported to the lake basin (Lane et al., 2011). The values of δ¹³C in the DKB core, ranging from ~27 to ~22‰, indicate that C₄ plants dominated the catchment through the Holocene (Fig. 6F) as they do today. The average δ¹³C value (pink horizontal lines in Fig. 6F) for DKB-I and DKB-II, particularly DKB-III, are notably higher than that of DKB-II, reflecting a change in vegetation composition between ~5270 and 2820 cal yr BP. The more positive δ¹³C values that characterize the DKB-III and DKB-I zones, especially the later portion of DKB-I (DBK-Ib: average level displayed by blue dashed lines), are inferred to reflect the increase of C₄ grasses growing along the margin of Lago Ditkebi. Muhlenbergia, the sole C₄ grass widely distributed in the Chirripó páramo today and found within the DKB catchment, is inferred to be the main source of terrestrial ¹³C input driving the variation in the δ¹³C records of Lago Morrenas 1, another glacial lake in Chirripó N.P. (Lane et al., 2011). Muhlenbergia, which can tolerate low temperatures, is largely restricted to relatively dry, coarse substrates in the Chirripó páramo (Lane et al., 2011). The more negative values of δ¹³C observed during DKB-II likely reflect a reduction in the abundance of Muhlenbergia along the lake’s shore, which could reflect Muhlenbergia occupying a habitat farther from the lake margin and the coring location, resulting in a decrease in the ¹³C contribution from the C₄ grass to the organic matter being transported into the lake. This interpretation supports the chironomid-based paleoecological inferences of elevated MAAT and higher lake level during this interval (Fig. 6F).

Variations in the stable isotope signature of δ¹³C, together with the chironomid-based inference of thermal conditions and the charcoal-based reconstruction of the local fire regime (Fig. 6), enable the development of an integrated proxy record of hydroclimate and environmental change spanning the past ~8100 years for the glacial highlands of Chirripó N.P. The abundance of cold-adapted chironomids together with minimal faunal turnover in zone DKB-I is inferred to reflect the occurrence of an interval of consistently low temperatures between ~8100 and 5270 cal yr BP. The occasional presence of terrestrial and semi-terrestrial taxa (e.g. Simitia/Pseudosmittia and Limnophyes) suggests that terrestrial/semi-terrestrial habitats were limited during this time. Variations in lake level (depicted as Horizon A in Fig. 7A), due to fluctuations in effective moisture, would occasionally lead to the development of terrestrial/semi-terrestrial habitat and thereby account for periodic presence of Simitia/Pseudosmittia and Limnophyes in DKB-I. In general, relatively enriched δ¹³C values during DKB-I indicate that Muhlenbergia expanded along the margin of the lake as a result of lowered lake levels and an expansion of suitable habitat, likely driven by relatively cold and dry conditions. Charcoal-inferred fire frequency is low, suggesting that this interval was very likely characterized by reduced convective activity and lightening-induced ignition.

The onset of DKB-II at ~5270 cal yr BP is punctuated by an abrupt increase in the thdermophilous chironomid, Polypedilum N type. The increase in Polypedilum N type, together with the presence of Simitia/Pseudosmittia and Limnophyes, suggest the occurrence of a short-lived interval of elevated rainfall, leading to increasing lake level and an expansion of terrestrial/semi-terrestrial habitats (Fig. 7B). Diamesa, a cold stenotherm that favors relatively low temperature (Brooks et al., 2007; Bouchard Jr and Ferrington Jr, 2009; Cranston, 2010; Anderson, 2012), first appears at Lago Ditkebi at ~5250 cal yr BP. An increase in lake level and volume would enhance stratification and enable the development of a deep pool of cold water suitable for Diamesa. Abrupt increases in CHAR and C/N at ~5250 cal yr BP also provides evidence for the occurrence of a large fire at this time. The up to 20 of C/N ratio is suggestive of an abrupt increase in the delivery of terrestrial organic matter to the lake, likely reflecting the occurrence of a catchment-scale disturbance (e.g. erosion and/or intense precipitation-induced surface runoff). The presence of a 1.5 cm-thick layer of large-size macroscopic charcoal (length/width range: 3000—5000 μm) and multiple large woody charcoal fragments as large as 0.25 cm² also the high concentration of woody and grass charcoal indicate that the fire that occurred at this time was intense and severe. Dwarf bamboo, which is abundant in the DKB catchment, would have provided sufficient fuel to support severe fires, and together with shrubs in the catchment, could have generated high amounts of woody charcoal. Limited fire activity during DKB-I would have as well as facilitated the buildup of fuel in the catchment of Lago Ditkebi and contributed to the severity of the fires at ~5250 cal yr BP. However, this severe fire observed at Lago Ditkebi site at ~5200 cal yr BP can be very local, because a simultaneous fire event was not evident in the sediments of Lago Morrenas 1, a large glacial lake located ~2.8 km to the northwest on the downwind site (League and Horn, 2000). The mobilization and transport of these large charcoal fragments to the lake basin located on the upwind slope would likely require intense precipitation and enhanced surface runoff, or extremely strong wind.

Following the severe fires at ~5250 cal yr BP, the continued presence of Polypedilum N type, which remains relatively high throughout zone DKB-II, reflects the occurrence of a persistent interval of elevated MAATs between ~5270 and 2820 cal yr BP. The reduction in the terrestrial/semi-terrestrial chironomid taxa Limnophyes and Smititia/Pseudosmittia between ~4900 and 3300 cal yr BP, together with the increased relative abundance of Diamesa, is inferred to be a response to an even deeper lake. An increase in lake level would increase the littoral zone expanse, accounting for the continued presence of Polypedilum N type and a reduction in terrestrial/semi-terrestrial habitat (Fig. 7C). Elevated temperature and increased lake level would promote stratification, resulting in the development of a deep, isolated pool of cold water in the profundal, providing a suitable habitat for Diamesa. The generally low δ¹³C values characterizing this interval are inferred to indicate the reduction in the abundance of Muhlenbergia in response to elevated temperature and lake levels (Fig. 7C). Fire peak frequency generally increases through zone DKB-II, although CHAR is relatively low between ~4900 and 3300 cal yr BP. Taken together, the multi-proxy analysis suggests that between ~4900 and 3300 cal yr BP, Lago Ditkebi was warm, relatively wet, and experienced frequent, low-severity fires. The termination of zone DKB-II, which is characterized by the re-appearance of Limnophyes and Smititia/Pseudosmittia, an increase in CHAR, fire frequency and disappearance of Diamesa, is inferred to reflect the onset of a gradual drying trend, decreasing lake levels and weakening stratification, beginning at ~3300 cal yr BP.

The composition of the chironomid assemblage and the δ¹³C values indicate that the environment of the last 2820 years at Lago Ditkebi (DKB-III) was cool and dry. The significant reduction of Polypedilum N type and the disappearance of Diamesa, together with the intermittent presence of Limnophyes and Smititia/Pseudosmittia, implies that Lago Ditkebi was characterized by fluctuating, but generally low lake levels during the late Holocene (Fig. 7D). The relatively high δ¹³C values reflect a synchronous expansion of Muhlenbergia within the catchment and support the interpretation of drier conditions. However, zone DKB-III differs from zone DKB-I in terms of the observed fire regime. Specifically, the high fire peak frequency of DKB-III indicates that wild fires were more active during the past ~2820 years, although the fires were of lower severity during the last ~1600 years. These fires may reflect increased human activities during the late Holocene in this region.
Fig. 7. Scenarios of Holocene hydroclimate and environmental change at Lago Ditkebi for: A) DKB-I (~8100–5270 cal yr BP); B) ~5200 cal yr BP; C) DKB-II (5270–2820 cal yr BP); and D) DKB-III (2820 cal yr BP-present).
Locations of study sites

1. Asia summer monsoon area (Morrill et al., 2003)
2. Sumai co, Tibetan Plateau (Gasse et al., 1991)
3. Lake Abiyata, Ethiopia (Challe and Gasse, 2002)
4. Neher Nile Valley, Egypt (Gasse, 2000 and 2002; Lancaster et al., 2002; Brooks et al., 2005)
5. Oﬀ Cap Blanc (marine core 658C), Mauritania (DeMenocal et al., 2000)
6. Bermuda Rise, Sargasso Sea (Keigwin, 1996)
7. Quelccaya ice cap, Peru (Thompson et al., 2006)
8. Huascaran ice cap, Peru (Thompson et al., 1995)
9. Little Salt Spring, the United States (Claussen et al., 1979)
10. Lakes Chiconahuapan and Chalco, Mexico (Street-Perrott and Perrott, 1990)
11. Lago Ditkabí, Costa Rica (This study)
12. Kilimanjaro, Tanzania (Thompson et al., 2002)
13. Soreq Cave, Israel (Bar-Matthews et al., 1997 and 1999)
15. Lago Palcacocha, Ecuador (Moy et al., 2002)
16. Lapa Grand Cave, Brazil (Strikis et al., 2011)
Holocene optima characterized by wet and warm conditions to late-lived notable cooling events or a hydroclimatic transition from mid-etal., 2006; Thompson et al., 2006; Brooks, 2010). Evidence of a short-lived event of an abrupt climate change event, inferred to be geochemistry, particularly C/N, and the high CHAR provides evidence of the occurrence of an abrupt climate change event, inferred to be featured with elevated temperature, increased precipitation and a severe fire at ~5200 cal yr BP (Fig. 8A, B–i–iv). During the past two decades, a growing number of studies conducted globally have identified an abrupt climate event at ~5000 cal yr BP (summarized in Magny et al., 2006; Thompson et al., 2006; Brooks, 2010). Evidence of a short-lived notable cooling event or a hydroclimatic transition from mid-Holocene optima characterized by wet and warm condition to late-Holocene characterized by cold and/or dry climate, particularly in Asia, Europe, and Africa (Fig. 8A, B) has been documented in the low latitudes. For example, a remarkable drop in δ13C values at ~5200 cal yr BP, recorded in the Kilimanjaro ice core (Tanzania), indicates an abrupt cooling occurred in tropical Africa (Fig. 8A, B–i; Thompson et al., 2002). Evidence showing a nearly simultaneous and significant hydroclimate variability is also found in speleothem records collected in Soreq Cave, Israel (Fig. 8A, B–vi; Bar-Matthews et al., 1997, 1999). Additional proxy records recovered from Lake Abiyata, Ethiopia (Fig. 8A–i); Chalié and Gasse, 2002) and Off Cap Blanc (marine core 658C), Mauritania (Fig. 8A–ii; deMenoca et al., 2000) indicate that climate quickly switched from wet to dry at ~5400 cal yr BP.

Studies from the tropical and subtropical Americas (Fig. 8A–ii–v, i–iv, v, ii, ix, x) show a greater diversity of responses to climate forcing at ~5200 cal yr BP. Rapid cooling at 5200 cal yr BP is documented at Bermuda Rise, Sargasso Sea (Fig. 8A–ii; Keigwin, 1996), Quelccaya ice cap (Fig. 8A–ii; Thompson et al., 2006) and Huascarán ice cap, Peru (Fig. 8A–iv; Thompson et al., 1995). In Mexico, a rapid lake level drop at ~5000 cal yr BP, followed by a rapid recovery, at lakes Chiconahualpan and Chalco, was inferred from variations in the diatom flora (Fig. 8A–ii); Street-Perrott and Perrott, 1990). However, signatures of abrupt warming and/or wetter conditions at ~5200 cal yr BP are also observed at multiple sites, including Little Salt Spring, southern United States (Fig. 8A–vii; Clausen et al., 1979), Laguna Ditkebi, Costa Rica (Fig. 8A–i, ii, iii, iv; this study), El Junco Lake, the Galapagos Islands (Fig. 8A–viii; vii, xii; Atwood, 2015), Laguna Pallcacocha, Ecuador (Fig. 8A, B–ix; Moy et al., 2002), and Lapa Grande Cave, Brazil (Fig. 8A, B–x; Stírskis et al., 2011). For example, Moy et al. (2002), reconstructed ENSO variability during the Holocene and identified an increase in convective precipitation along the western slope of the Andes at ~5000 cal yr BP. Additionally, non-ENSO related rainfall in the eastern tropical Pacific also increased at ~5200 cal yr BP in the Galapagos Islands (Fig. 8A, B–vii, viii; Atwood, 2015).

A mechanism accounting for the expression of the abrupt climate event at ~5200 cal yr BP remains elusive (Mayewski et al., 2004; Chiang and Bitz, 2005; Staubwasser and Weiss, 2006; Thompson, 2011; Chiang and Friedman, 2012; Chiang et al., 2014). The correspondence between insolation variation and this abrupt climate change observed at ~5200 cal yr BP in Costa Rica appears limited (Fig. 8B–xii). It has been proposed that an anomalous temperature in the tropical North Atlantic at this time reduced the inter-hemispheric temperature gradient, resulting in the northward migration of the ITCZ and increased precipitation in the northern tropical Americas (Broccoli et al., 2006; Schneider et al., 2014). A more northerly positioned ITCZ would increase cloud coverage over the tropical North Atlantic, reduce the loss of longwave radiation and further warm the surface ocean in tropical North Atlantic (Xie and Carton, 2004; Chiang and Friedman, 2012).

6. Conclusions

This high-resolution, multi-proxy record from Lago Ditkebi, provides evidence that the glacial highlands of Costa Rica were featured with 1) relatively cold, dry conditions, decreased effective moisture, and limited fire activity between ~8100 and 5270 cal yr BP, 2) persistent elevated temperature, increased effective moisture and frequent, high-severity fires between ~5270 and 2820 cal yr BP, and 3) cool, dry conditions, and frequent low-severity fires between ~2820 cal yr BP and present. Macroscopic charcoal analysis, which indicates that wildfires periodically burned the study site throughout the Holocene, also documents the occurrence of a severe fire event at ~5270 cal yr BP and high fire frequency between ~3300 and 1600 cal yr BP. Existence of an abrupt climate change event centered at ~5200 cal yr BP is evidenced by the synchronous response of chironomids, C/N and CHAR. A holistic consideration of these proxies suggests that this interval was characterized by relatively warm, increased precipitation and possibly, enhanced thunderstorm activity. The finding for the 5200 cal yr BP event in the glacial highlands of Costa Rica corresponds well with other paleoclimate records from the low-latitudes and provides support for the hypothesis that the enhanced convection, rainfall and thunderstorm activity observed at Lago Ditkebi was driven by an increase in temperature-dependent evaporation, resulting from increased SSTs, and amplified moisture transport in the northern tropical Americas at ~5200 cal yr BP.

Acknowledgments

This research was supported by a Provost Summer Research Award to David F Porinchu from the University of Georgia (UGA), two Graduate Student Research Grants from Geological Society of America and grants from the crowdfunding platform Experiment.com to Jiaying Wu. We would like to thank Jose Luis Garita for his assistance in the field and Dr. Tom Maddox at the Center for Applied Isotope Studies at UGA for providing guidance and conducting the geochemistry analyses. We would also like to thank Drs. Steve Padgett-Vasquez, Germain...