Research paper

The Holocene
2017, Vol. 27(1) 73–84

DOI: 10.1177/0959683616652702
hol.sagepub.com
SAGE

A chironomid-based reconstruction of late-Holocene climate and environmental change for southern Pacific Costa Rica

Jiaying Wu,[1] David F Porinchu[1] and Sally P Horn[2]

Abstract

A lake sediment profile spanning the last ~3200 years from Laguna Zoncho in the southern Pacific region of Costa Rica was analyzed for sub-fossil chironomids. Notable shifts in chironomid assemblages occurred during the late-Holocene. A distinct chironomid community, dominated by Tanypodinae such as *Procladius* and *Labrundinia*, appeared after ~550 cal. yr BP (~1400 CE). Prior to this time, the chironomid assemblage was more diverse, with taxa such as *Paratanytarsus, Tanytarsus* type N, and *Cladotanytarsus* important constituents of the chironomid community. A chironomid-based inference model for mean annual air temperature (MAAT), developed using partial least squares (PLS 2-component), was applied to sub-fossil chironomid assemblages from Laguna Zoncho to reconstruct late-Holocene thermal variability for the region. The key findings from this study are as follows: (1) chironomid-inferred MAAT at ~2740–1220 cal. yr BP (790 BCE–730 CE) was 1.2°C higher than the late-Holocene (~3200 cal. yr BP to present in this study) average of 21.3°C; (2) MAAT at ~470–90 cal. yr BP (1480–1860 CE) was 1.3°C lower than the late-Holocene average, potentially reflecting 'Little Ice Age' (LIA) cooling; and (3) evidence for an extended period of low lake levels between 1220 and 840 cal. yr BP (730–1110 CE) possibly indicated the influence of the Terminal Classic Drought (TCD) in southern Costa Rica. This study pioneers the use of sub-fossil chironomid remains to develop quantitative estimates of Holocene thermal variability and environmental change in Central America.

Keywords

chironomid, Costa Rica, Late-Holocene, 'Little Ice Age', paleoclimate, temperature, Terminal Classic Drought

Received 12 June 2015; revised manuscript accepted 18 April 2016

Introduction

Investigations of sediment records recovered from lakes in Costa Rica have provided important insights into the nature of tropical climate and landscape change and refined our understanding of tropical climate variability in southern Central America during the latest Pleistocene and Holocene. Multi-proxy paleoenvironmental studies document a notable decrease in mean annual air temperature (MAAT) during the Last Glacial Maximum (LGM) and considerable climate variability during the Holocene (Horn, 2007). For example, pollen analysis of sediment extracted from La Chonta bog (2310 m a.s.l.), located in the northern Cordillera de Talamanca of Costa Rica, suggested that MAAT was 7–8°C lower than the present between ~50,000 and 15,600 cal. yr BP (Hooghiemstra et al., 1992; Horn, 2007), in close agreement with estimates from reconstructions of paleoglaciers at higher elevations in the Cordillera de Talamanca (Lachniet and Seltzer, 2002; Orvis and Horn, 2000). At La Chonta bog, the late glacial (15,600–12,900 cal. yr BP) was characterized by an increase of approximately 4.6°C in MAAT and increases in annual precipitation and the upper forest line (Hooghiemstra et al., 1992), although warming was interrupted by an event thought to be correlative with the Younger Dryas (12,900–11,600 cal. yr BP). Pollen evidence from La Chonta and La Trinidad bogs indicates that the early- and middle-Holocene (10,700–5200 cal. yr BP) at mid-elevations in the Cordillera de Talamanca was characterized by higher effective moisture and relatively stable thermal conditions (Horn, 2007; Islebe et al., 1996). Pollen and charcoal stratigraphies developed for lakes on the glaciated Chirripó massif of Costa Rica indicate that these uplands were dominated throughout the Holocene by treeless páramo similar to the present and characterized by periodic fires (Horn, 1993; League and Horn, 2000), especially during the late-Holocene. Increased burning during the late-Holocene is interpreted to reflect drier conditions as compared with the middle-Holocene, when charcoal is sparse in lake sediments. This interpretation is in keeping with evidence of vegetation changes at the bog sites (Islebe et al., 1996) and with carbon and hydrogen isotope records from Morrenas Lake 1 (Lane and Horn, 2013; Lane et al., 2011a). In the sediments of Lago Chirripó, two distinct layers of macroscopic charcoal suggest intervals of lower lake level at about 1100 and 2500 cal. yr BP (Horn, 1993) that may be associated with regional droughts (Hodell et al., 2000, 2001; Horn, 2007; Lane et al., 2014).

Although much valuable paleoecological and paleoclimatological research has been conducted in Costa Rica, an outstanding opportunity exists to extend our current understanding of late-Holocene climate change in the southern Pacific region using sub-fossil chironomid analysis to develop quantitative reconstructions of late-Holocene thermal conditions. Sub-fossil chironomid analysis has proven to be valuable in developing

---

[1]Department of Geography, The University of Georgia, USA
[2]Department of Geography, The University of Tennessee, USA

Corresponding author:
Jiaying Wu, Department of Geography, The University of Georgia,
Athens, GA 30605, USA.
Email: wu1092@uga.edu

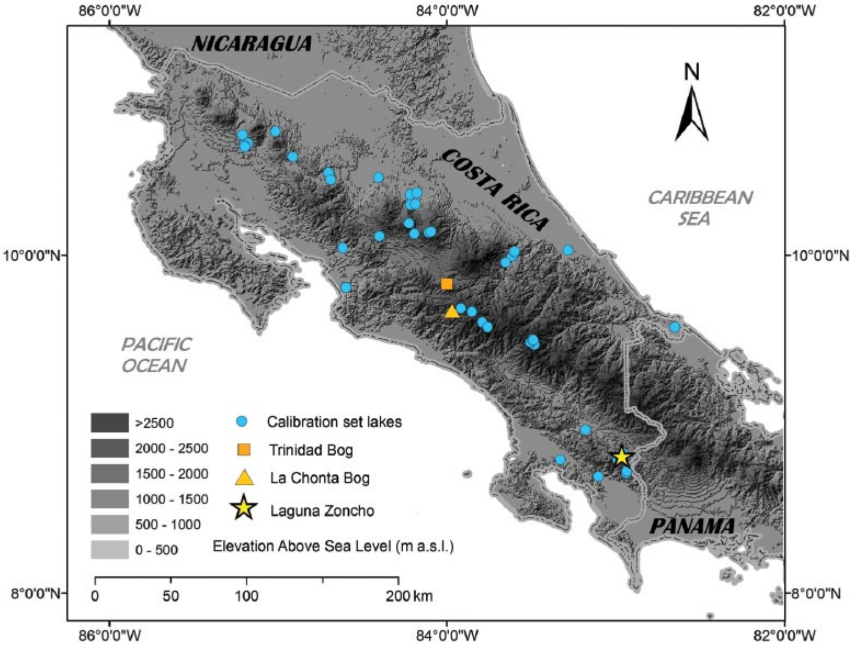

Figure 1. Locations of paleoenvironmental records referenced in the text, the 51 lakes in the Costa Rican chironomid calibration set and Laguna Zoncho (Wu et al., 2015).

quantitative temperature reconstructions for the late Quaternary (Porinchu and MacDonald, 2003; Walker, 2001; Walker and Cwynar, 2006). Chironomids are sensitive indicators of past temperature and offer great potential to provide independent estimates of regional climate conditions during intervals of transition (Axford et al., 2009; Engels et al., 2008; Levesque et al., 1997; Reinemann et al., 2014). The existence of strong, statistically significant correlations between chironomid assemblages and temperature (surface water and air) has facilitated the development of chironomid-based inference models from the high-, mid-, and low-latitudes (e.g. Barley et al., 2006; Heiri et al., 2011; Porinchu et al., 2010; Self et al., 2011; Wu et al., 2015). Application of inference models to sub-fossil chironomid stratigraphies has enabled researchers to develop quantitative paleotemperature reconstructions with high temporal resolution in much of North America, Eurasia, and increasingly in Asia, Africa, and South America (Eggermont et al., 2010; Ilyashuk and Ilyashuk, 2007; Ilyashuk et al., 2011; Massaferro et al., 2009; Reinemann et al., 2009); however, qualitative and quantitative chironomid-based paleoenvironmental reconstructions in Central America remain limited.

Wu et al. (2015) documented the modern relationship between chironomid distribution and limnological and climatic parameters in Costa Rica. Direct gradient analyses indicated that MAAT is strongly correlated to the distribution of chironomid taxa in the 39 Costa Rican lakes included in the study. The robust performance statistics of the two-component partial least squares (PLS) chironomid-based MAAT inference model ($r^2_{\text{jack}} = 0.94$, RMSEP = 1.73°C) supports using this model to reconstruct Holocene thermal regimes in Costa Rica and potentially elsewhere in Central America. In this paper, we apply the quantitative chironomid-based inference model developed by Wu et al. (2015) to sub-fossil chironomid assemblages extracted from a sediment core recovered from Laguna Zoncho in southern Pacific Costa Rica to develop a qualitative reconstruction of environmental change and a quantitative estimate of thermal variability for this region spanning ~3200 years. Comparison of the sub-fossil chironomid-based reconstructions to existing paleoclimate records from the region enables us to determine the degree of correspondence between thermal variability and landscape change and to explore how chironomid evidence of late-Holocene climate at Laguna Zoncho links to other evidence of climate and environmental changes in Costa Rica and the broader tropical region.

Study site

Laguna Zoncho (8.8121°N, 82.9607°W) is a small (0.75 ha), mid-elevation (1190 m a.s.l.) lake located on the eastern end of the Fila Costeña mountain range, near the Panamanian border in southern Pacific Costa Rica (Figure 1). The site is within the Diquís subregion of the Greater Chiriquí archaeological region, which includes southern Pacific Costa Rica and western Panama. Laguna Zoncho is underlain by Tertiary volcaniclastic sedimentary rocks (Ortiz, 2005) and formed at 3200 cal. yr BP by large-scale slumping, faulting, or both (Clement and Horn, 2001). The lake is on the grounds of a private nature reserve, Finca Cantaros, which is open to the public and includes an ornamental garden and slopes reforested over the last two decades following earlier cattle grazing and coffee cultivation at the site (Horn and Haberyan, 2016). The lake and surroundings fall within the premontane wet forest and premontane rain forest transition life zones according to the Holdridge bioclimatic classification (Holdridge et al., 1971; Ortiz, 2005). While much of the area has been cleared since the 1950s for pasture and crop cultivation, the Organization for Tropical Studies' Las Cruces Biological Station located 3 km south of the lake includes several hundred hectares of remnant and regenerating forests (http://ots.ac.cr/index.php?option=com_content&task=view&id=220&Itemid=422). Following the Köppen classification, the region can be characterized as having a humid, equatorial climate with a dry winter. Data from the Loma Linda meteorological station located 9 km SSE of Laguna Zoncho (8.8121°N, 82.9607°W; elevation 1180 m a.s.l.) show mean annual temperature and mean annual precipitation for the period 1988–2007 are 20.5°C and 3359 mm, respectively (http://www.ots.ac.cr/meteoro/default.php?pestacion=3). During that period, 88% of the annual precipitation fell during the wet season from May to November.

Methods

We analyzed chironomids in samples from the lacustrine section (0–2.9 m) of a 5.9-m sediment core that was recovered from near the center of Laguna Zoncho in March 1997. At the time of coring, the lake level was low, with a depth of only 2.3 m at the core site, but repeated visits for limnological sampling (Horn and Haberyan, 2016) and additional coring (Taylor et al., 2015) have revealed lake levels up to 2 m higher. In 1997, the watery upper

Table 1. AMS ^{14}C dates available for the Laguna Zoncho lake sediment core. Analyses were performed by Beta Analytic Laboratory on small wood fragments (W) or mixtures of charcoal, seeds and leaf fragments (M). Radiocarbon ages were calibrated using CALIB 7.02 and the data set of Reimer et al. (2013).

Lab no.	Depth (cm)	Material dated	Uncalibrated ^{14}C age (^{14}C yr BP)	±	Median (cal. yr BP)	Calibrated age ± 1σ (cal. yr BP)	Calibrated age ± 2σ (cal. yr BP)
β-122556	118–122	M	540	50	558	518–558 602–629	505–569 582–650
β-122555	248–250	M	2110	50	2086	2004–2028 2035–2145	1949–2180 2241–2303
β-115186	283–284.5	W	2940	50	3095	3005–3015 3021–3065	2948–3238 3313–3316

sediments (0–1.13 m) were sampled using a plastic tube fitted with a rubber piston and extruded, sub-sectioned, and bagged in the field at 2 cm intervals, and deeper sediments were recovered using a Colinvaux-Vohnout locking piston corer (Colinvaux et al., 1999). Core sections were returned to the Laboratory of Paleoenvironmental Research at the University of Tennessee still encased in the original 1-m-long aluminum coring tubes. In the lab, the tubes were opened on a modified router and the core sections were sliced longitudinally for sampling, initially for pollen and microscopic charcoal and loss-on-ignition (Clement and Horn, 2001) and later for stable carbon isotopes (Lane et al., 2004), diatoms (Haberyan and Horn, 2005), phosphorous (Filippelli et al., 2010), and finally chironomids (this study).

The 1997 Laguna Zoncho sediment core contains a lower section composed mainly of mineral regolith with poor pollen preservation and a pollen-rich lacustrine section (0–290 cm) (Clement and Horn, 2001). Chronological control for the lacustrine profile is based on three AMS dates on small wood fragments or samples containing a mixture of charcoal, seeds, and leaf fragments and a well-dated tephra layer from the volcano Barú in western Panama (Table 1 and see Clements and Horn, 2001 for additional details). For this paper, the radiocarbon dates were converted to calendar ages using CALIB 7.1 and the data set of Reimer et al. (2013). Ages were estimated using a linear age model and the weighted means of the probability distributions of the calibrated ages. Based on the age model, the lacustrine sediment in the core accumulated slowly (0.034 cm yr^{-1}) between ~3100 and 2100 cal. yr BP (284–249 cm) and more quickly (0.084 cm yr^{-1}) between 2100 and 560 cal. yr BP (247–120 cm) and (0.194 cm yr^{-1}) from 540 cal. yr BP to the present. The highest sedimentation rate (1.013 cm yr^{-1}), which occurred between 560 and 540 cal. yr BP (120–99.75 cm), was likely due to the eruption of Volcano Barú (located 35 km east of the study site).

Chironomid samples were analyzed at ~10 cm resolution in the upper 290 cm of the core. A minimum of 50 head capsules were analyzed for each interval, with the exception of samples at 272 and 287 cm for which 46 and 44 head capsules were enumerated, respectively. The chironomid analysis was conducted following standard procedures outlined in Walker (2001). The sediment was treated with 5% KOH solution to facilitate the break-up of colloidal matter. A known volume of sediment (3–8 mL) was placed in a beaker with 50 mL of 5% KOH and heated at 50°C for approximately 30 min. The deflocculated sediment was washed through a 95-µm mesh and rinsed using distilled water. The material retained on the mesh was backwashed into a beaker. A dissection microscope at 50× magnification and a Bogorov plankton counting tray were used to separate the chironomid head capsules from the sediment matrix. The chironomid head capsules were permanently mounted on slides in Entellan© for identification. Taxonomic identification was conducted at 400× magnification, typically to genus, relying primarily on larval keys for Florida and North and South Carolina (Epler, 1995, 2001), with Brooks et al. (2007), Eggermont et al. (2008), and Cranston (2010) providing additional diagnostic information.

The chironomid percentage diagram, plotted using C2 (Juggins, 2003), was based on the relative abundance of all identifiable chironomid remains. Taxon richness was determined by counting the number of distinct taxonomic groupings in each sample. We numerically zoned the chironomid percentage diagram based on optimal sum-of-squares partitioning, using the R-based rioja package (Juggins, 2014). The degree of turnover in the sub-fossil chironomid assemblages can be indicated by the shift of the assemblage data-based detrended correspondence analysis (DCA) curve. A chironomid-based inference model (2-component PLS) for MAAT (Wu et al. 2015) was applied to this data set. This inference model is based on 45 chironomid taxa in surface samples from 39 lakes that span seven ecosystem regions and elevations from 10 to 3520 m a.s.l. and provides robust performance statistics ($r^2_{\text{jack}} = 0.94$, RMSEP = 1.73°C). Application of the inference model to the Laguna Zoncho chironomid stratigraphy provides a means to develop a quantitative temperature reconstruction spanning the late-Holocene for the region. Reconstructions are based on sub-fossil chironomid assemblages that have >95% of the sub-fossil taxa present in the calibration set, which are considered reliable (Birks, 1998). The reliability of the quantitative chironomid-based reconstruction was also evaluated by determining (1) the dissimilarity between each Zoncho chironomid sample and its closest modern analog using a modern analog technique (MAT-ech) approach based on a minimum dissimilarity chord distance and (2) square residual goodness-of-fit (GOF) of each Zoncho chironomid assemblage to the first ordination axis in a canonical correspondence analysis (CCA) constrained solely by MAAT. The second and fifth percentiles of the distribution of dissimilarities, based on the calibration set samples incorporated in Wu et al. (2015), were used to define the cut-off for 'no close' and 'no good' analogs, respectively (Birks et al., 1990; Engels et al., 2008; Heiri et al., 2003). Samples with a squared residual distance greater than the 90th, 95th and 99th percentiles of the residual distances of the calibration set samples were identified as having a 'poor fit' or 'extremely poor fit' with temperature, respectively (Birks et al., 1990). The trajectory of change in the sub-fossil chironomid assemblages in Laguna Zoncho was determined using correspondence analysis (CA), with the sub-fossil chironomid assemblages plotted passively against the modern calibration set samples (Wu et al. 2015).

Results

Sub-fossil chironomid head capsules were well preserved in the lacustrine sediments of the Zoncho core except for the interval between 176 and 144 cm. A total of 24 chironomid taxa were identified, with 23 taxa present (>95%) in the modern calibration set (Wu et al., 2015). *Tanytarsus* type W (Figure 3) is the only taxon, present in the sub-fossil chironomid assemblages from Laguna Zoncho, not found in the modern calibration set. Chironomid richness varied between 4 and 18 with the highest taxon richness occurring at approximately 1400 cal. yr BP (550 CE). *Chironomus, Labrundinia*, and *Procladius* were the most abundant chironomid taxa. The chironomid stratigraphy is divided into four zones (Figure 2).

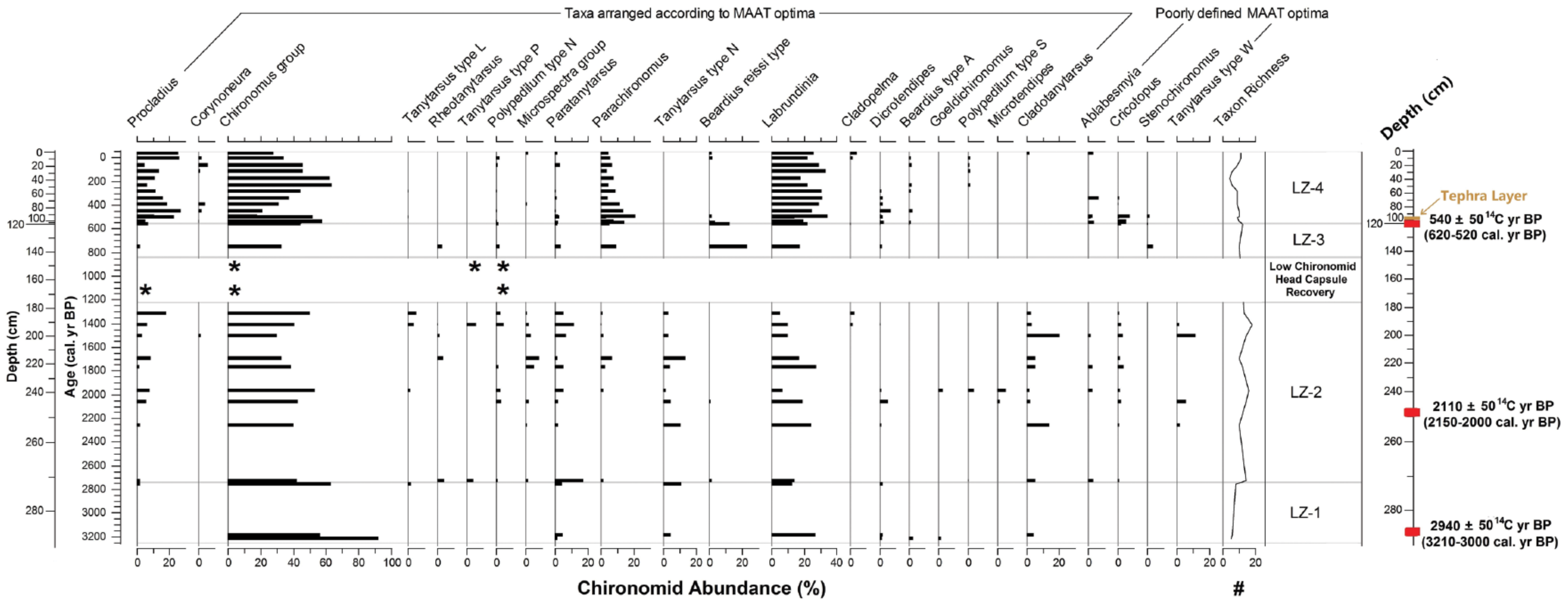

Figure 2. Sub-fossil chironomid stratigraphy for Laguna Zoncho. Taxa on the left side of diagram are arranged according to MAAT optima as determined by Wu et al. (2015), with *Procladius* having the lowest MAAT optima and *Cladotanytarsus* having the highest MAAT optima. The taxa observed in the 'Low Chironomid Head Capsule Recovery' interval are symbolized by asterisks. The locations of the radiocarbon dates are indicated by red bars on the right margin of the figure, labeled with uncalibrated ^{14}C age and calibrated age range (cal. yr BP ±1σ) in brackets (see Clements and Horn, 2001 for additional details). The location of tephra layer is marked by brown bar.

Zone LZ-1 (~3220–2740 cal. year BP or 1270–790 BCE; 288–271.5 cm)

This zone is dominated by two taxa: *Chironomus* and *Labrundinia*. Lesser amount of taxa belonging to the sub-tribe Tanytarsini – *Cladotanytarsus, Paratanytarsus*, and *Tanytarsus* type N – are also present. Taxon richness is relatively low with only nine taxa present in this zone (Figure 2). *Chironomus* is most abundant in mid-elevation lakes (1000–2000 m a.s.l.) today in Costa Rica (Wu et al., 2015). The other taxa present in LZ-1, such as *Dicrotendipes, Labrundinia, Beardius* type A, and *Paratanytarsus*, are most abundant and common in warm, low-elevation lakes (Wu et al., 2015). The DCA suggests that limited faunal turnover occurred during this interval (Figure 4a).

Zone LZ-2 (~2740–1220 cal. yr BP or 790 BCE–730 CE; 271.5–176 cm)

This zone is characterized by a more diverse chironomid community with taxon richness reaching a profile maximum of 18 at approximately 1400 cal. yr BP (550 CE). Thermophilous taxa are particularly abundant. The assemblage in LZ-2 is dominated by *Chironomus*, which co-occurs with less amounts of *Labrundinia* (Figure 2). Taxa that are associated with warm, low-elevation lakes, such as *Paratanytarsus, Polypedilum* type N, *Micropsectra, Labrundinia, Cladotanytarsus* and Tanytarsus type N, are frequent in this zone (Wu et al., 2015). Taxa such as *Parachironomus, Procladius, Cricotopus*, and *Corynoneura* are also present in this zone, but at low relative abundance. The increase in the relative abundance of *Procladius* along with the decrease in the relative abundance of *Labrundinia* and *Tanytarsus* N type at the very top of LZ-2 is inferred to indicate the onset of a decrease in air temperature at the termination of this zone. Today, *Procladius* is most abundant in cold, high-elevation lakes (>3000 m a.s.l.) in Costa Rica, whereas *Labrundinia* and *Tanytarsus* type N are most abundant in mid- and low-elevation lakes (Wu et al. 2015). A previously undescribed chironomid taxon is also observed in LZ-2: *Tanytarsus* type W is characterized by sharply sloping first lateral teeth, which serves as the key diagnostic feature (Figure 3). Additional diagnostic features include the presence of a single narrow median tooth with one pair of tiny supplementary teeth, a mandible with two inner teeth, and an antennal pedestal with a round and pointed spur. *Cladopelma*, a chironomid absent today from lakes located higher in elevation than Laguna Zoncho, appears for the first time in the record at the top of LZ-2, immediately prior to a distinctly different interval in the Zoncho chironomid record. The DCA indicates that the chironomid community experienced limited faunal turnover until ~1220 cal. yr BP (Figure 4a). Low chironomid interval (~1220–840 cal. yr BP or 730–1110 CE; 176–144 cm) between zones LZ-2 and LZ-3 in the Zoncho profile is a section of sediment with only sparse chironomid head capsules indicating an interval of low chironomid abundance. The number of sub-fossil chironomid head capsules recovered in samples from this interval failed to meet the screening criteria required for further statistical analysis, precluding the use of these samples in deriving quantitative estimates of MAAT. However, the taxa that are present between 1220 cal. yr BP and 840 cal. yr BP, such as *Cladotanytarsus, Tanytarsus* type P, and *Rheotanytarsus*, typically occur in the littoral of warm, productive, low-elevation lakes in Costa Rica today (Wu et al., 2015).

Rapid compositional change is often a signal of notable fluctuation in limnological and/or environmental conditions. The DCA of the chironomid percentage data indicates that the chironomid community at Laguna Zoncho experienced one major interval of rapid turnover during the late-Holocene (Figure 4a). This interval occurred during the transition between LZ-2 and LZ-3. The chironomid community in LZ-2 was dominated by taxa associated with warm, low-elevation lakes such as *Paratanytarsus, Polypedilum* type N, *Micropsectra, Labrundinia, Cladotanytarsus*, and *Tanytarsus* type N. Following LZ-2, the relative abundance of *Micropsectra* and *Cladotanytarsus* declined and the relative abundance of taxa commonly associated with aquatic macrophytes and wetland habitats such as *Stenochironomus* and *Beardius reissi* type increased in the LZ-3 (Figure 2). It is important to note that the chironomid community during the transition between LZ-2 and LZ-3 was characterized by a ~400-year-long interval of low lake productivity with sub-fossil chironomid remains extremely scarce (average <1.6 heads/mL) in the sediments between ~1220 and 840 cal. yr BP (~730–1110 CE).

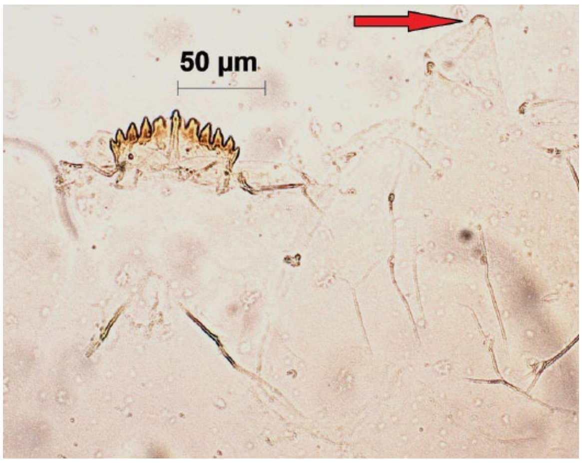

Figure 3. Photomicrograph of *Tanytarsus* type W, a previously undescribed chironomid taxon in Costa Rica. The key diagnostic features of this taxon are the sloping angle of the outer margin of the first pair lateral teeth and the presence of an antennal pedestal with a round and pointed spur (arrow).

Zone LZ-3 (~840–550 cal. yr BP or 1110–1400 CE; 144–108 cm)

Taxon richness decreases to an average value of 12 in Zone LZ-3 (Figure 2). The decrease in taxon richness is largely driven by a reduction in the relative abundance of taxa typically associated with warm, low-elevation lakes (e.g. *Micropsectra* and *Cladotanytarsus*), and the local extirpation of multiple *Tanytarsus* taxa, for example, *Tanytasus* type P, *Tanytarsus* type L, and *Tanytarsus* type N; *Tanytarsus* type P, and *Tanytarsus* type N, is most commonly associated with low-elevation lakes (Wu et al., 2015). Zone LZ-3 is also characterized by a notable increase in *Beardius reissi* type and the appearance of *Stenochironomus* taxa that are often associated with submerged macrophytes and littoral vegetation, respectively (Cranston, 2010). The modern calibration set documents that *Stenochironomus* and *Beardius reissi* type are most abundant in and commonly associated with warm, low-elevation lakes in Costa Rica (Wu et al., 2015). *Chironomus* (50%) continues to dominate this zone. The DCA suggests that a notable amount of faunal turnover characterized the chironomid community during the transition through the interval with extremely low chironomid head capsule recovery (Figure 4a).

Zone LZ-4 (~550 to −47 cal. yr BP or ~1400–1997 CE; 108–0 cm)

The relative abundance of *Chironomus*, which continues to be high in this zone, fluctuates between 20% and 60% of identifiable chironomid remains (Figure 2). This zone is characterized by a noticeable increase in *Cricotopus*, a taxon commonly associated with high-elevation lakes (Wu et al., 2015). Warm water taxa, such as *Labrundinia, Chironomus, Dicrotendipes*, and

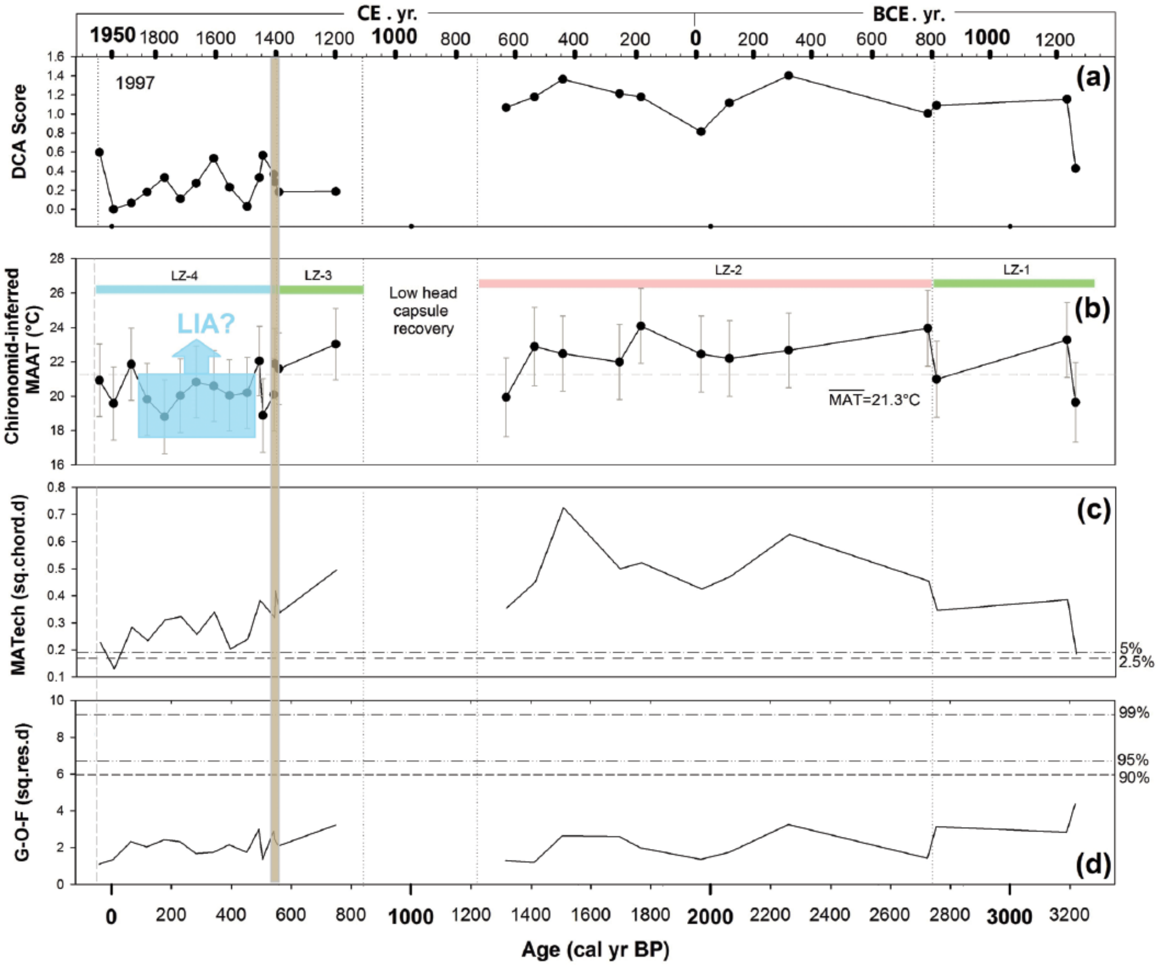

Figure 4. (a) Detrended correspondence analysis (DCA) first axis score based on the sub-fossil chironomid assemblages in the Laguna Zoncho core. (b) Chironomid-inferred MAAT reconstruction for Laguna Zoncho site (solid line with gray error bars). (c) Square chord dissimilarity distance (sq. chord. d) to the nearest modern analogs (MATech) in Wu et al. (2015). (d) The goodness-of-fit (GOF) of the fossil samples to a canonical correspondence analysis (CCA) constrained solely to temperature. Horizontal lines in the GOF analysis indicate the 90th (dash line), 95th (dash-dot-dot line), and 99th (dash-dot line) percentiles in residual distances of the modern samples to the first axis in a constrained CCA and are defined as 'poor fit', 'very poor fit', and 'extremely poor fit', respectively (Birks et al., 1990). Vertical brown bar represents the Barú tephra layer observed between 99 and 100.5 cm and dated to ~538 cal. yr BP (Taylor et al., 2013a).

Ablabesmyia, are also observed in this zone, indicating the existence of a diverse chironomid community during this interval (Wu et al., 2015). The local extirpation of *Stenochironomus* and *Rheotanytarsus* and a notable reduction in the relative abundance of *Beardius reissi* type occurs in LZ-4. *Stenochironomus* and *Beardius reissi* type are often associated with submerged aquatic macrophytes and wetland vegetation (Jacobsen and Perry, 2000; Pinder and Reiss, 1983), whereas *Rheotanytarsus* is commonly found in inflowing water (Pinder and Reiss, 1983). Taxon richness increases to 18 in LZ-4; however, the recently deposited sediment (~1950–1997 CE; 10–0 cm) is characterized by initially decreased and then increased taxon richness (Figure 2). The DCA indicates relatively limited faunal turnover characterizes LZ-4, although sample-to-sample fluctuations are observed (Figure 4a).

The chironomid-based quantitative MAAT reconstruction for Laguna Zoncho is presented in Figure 4b. The temporal resolution of the sub-fossil chironomid assemblage analysis and the associated quantitative temperature reconstruction vary from sub-centennial scale (550 cal. yr BP–present) to centennial scale (2300−550 cal. yr BP) and to multi-centennial scale (3200−2300 cal. yr BP). Reconstructed MAAT varied from a minimum of 18.8°C at 180 cal. yr BP (~1770 CE) to a maximum of 24.1°C at around 1770 cal. yr BP (~180 CE), with 21.3°C as the average MAAT for late-Holocene (~3200 cal. yr BP to the present in this study). The chironomid-inferred MAAT reconstruction suggests that Laguna Zoncho experienced warmer interval between ~2740 and 1220 cal. yr BP (Figure 4b, LZ-2, highlighted in light red) and colder interval from 550 to −47 cal. yr BP (~1400–1997 CE, Figure 4b, LZ-4, highlighted in light blue). Specifically, the reconstructed MAAT from ~2740 to ~1220 cal. yr BP (790 BCE–730 CE) was averagely 22.5°C, that is, 1.2°C higher than the late-Holocene average, and from 550 to −47 cal. yr BP was 20.4°C, that is, 0.9°C lower than the late-Holocene average (Figure 4b). Sample-specific error estimates ranged between 2.0°C and 2.3°C. Analyses of the reliability of the quantitative chironomid-based temperature reconstruction using modern analog technique (MATech) and GOF approaches gave mixed results (Figure 4c and d). The GOF analysis indicates that the sample scores fluctuate below the 90th percentile cut-levels and therefore have a good fit to temperature and can be considered reliable. However, the MATech analysis indicates that close analogs in the modern calibration set (Wu et al., 2015) are limited to the chironomid assemblages recovered from the uppermost (~1950 CE) and lowermost (~3200 cal. yr BP) portions of the profile.

Discussion

Paleoecological and paleolimnological analyses of the sediment of Laguna Zoncho have provided important insight into late-Holocene environmental change for the southern Pacific region

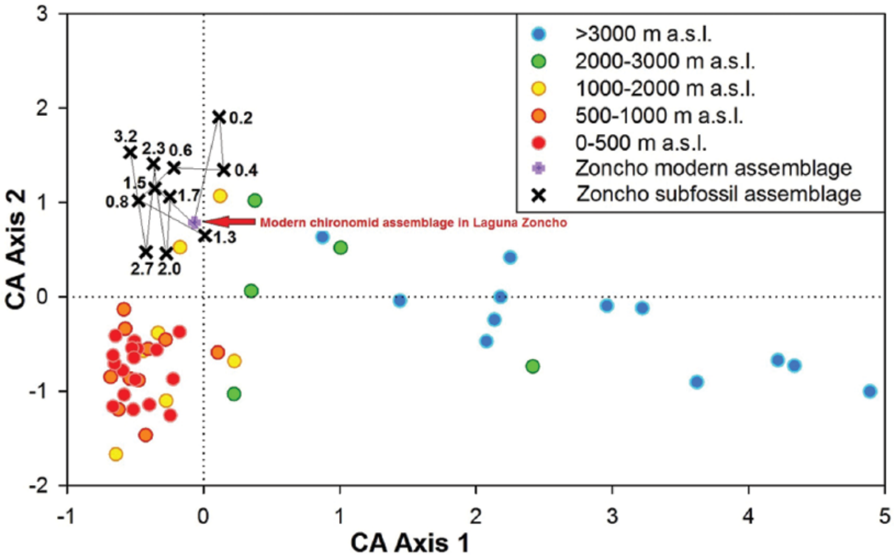

Figure 5. Time-trend CA biplot comparing sub-fossil chironomid assemblages from Laguna Zoncho with the modern chironomid assemblages in the 51-lake calibration set from Costa Rica (Wu et al. 2015). The calibration data set lakes are classified according to elevation (m a.s.l.). Numeric values near the black crosses in the diagram represent Zoncho sub-fossil assemblages at ~0.2 kyr interval from 2.0 k cal. yr BP to modern time and at 0.3–0.5 kyr interval from 3.2 to 2.0 k cal. yr BP (coarser time interval is due to lower temporal resolution at the base of the core).

of Costa Rica (Clement and Horn, 2001; Filippelli et al., 2010; Haberyan and Horn, 2005; Lane et al., 2004; Taylor et al., 2013b). These studies documented the onset and magnitude of prehistoric agriculture, the timing of subsequent forest recovery, and the changes in catchment conditions and lake productivity that result from agricultural and associated anthropogenic activities. Aspects of these records also suggested possible climate-driven shifts in environment and human activities (Taylor et al., 2013a). Deciphering the paleoecological information contained within the sub-fossil chironomid assemblages extracted from Laguna Zoncho provides an additional means to characterize late-Holocene environmental and climate change in the neotropics and application of a quantitative inference model for MAAT (Wu et al., 2015) to the Laguna Zoncho chironomid stratigraphy may help elucidate the role of temperature in driving the inferred changes. The resolution of the original chronology (Clement and Horn, 2001), based on three radiocarbon dates, has been increased with the inclusion of an additional date, which is associated with the presence of a tephra layer (dated at ~538 cal. yr BP) from the eruption of volcano Barú located at western Panama. It is important to recognize that chronological control for the Laguna Zoncho sediment sequence is most robust at centennial-scale resolution.

The trajectory of change in the sub-fossil chironomid assemblages in Laguna Zoncho was determined by passively plotting the sub-fossil chironomid assemblages against the modern calibration set samples using correspondence analysis (CA) (Figure 5). The black crosses represent the movement of the chironomid assemblages relative to the modern chironomid community (classified by elevation) at a multi-centennial time scale during the late-Holocene (Wu et al., 2015). The modern chironomid assemblage recovered from Laguna Zoncho is most similar to assemblages found today in mid-elevation lakes with moderate MAAT. The ordination diagram, which separates cold, high-elevation lakes from warmer, low-elevation lakes along CA axis 1, suggests that the sub-fossil assemblages found throughout the Laguna Zoncho record are most similar to assemblages found in warm, productive, low, and mid-elevation lakes today and that the changes in MAAT that occurred at Laguna Zoncho during the past 3200 years were relatively muted. However, the CA indicates that notable changes in the trajectory of the sub-fossil chironomid assemblages with respect to temperature occurred between 1300 and 800 cal. yr BP and between 600 and 400 cal. yr BP. The movement of the sub-fossil chironomid assemblage at 1300 cal. yr BP toward the assemblages that characterize the lowest elevation lakes today is inferred to reflect an increase in MAAT during this interval. The sub-fossil chironomid assemblages, which move toward the assemblages that characterize high-elevation sites today between 400 and 200 cal. yr BP, are inferred to reflect a decrease in MAAT during this interval.

It is important to recognize that changes in the lake catchment, related to agricultural activity and vegetation composition, may have influenced the chironomid community at Laguna Zoncho. A DCA of the pollen data, which captures the magnitude and timing vegetation change, was used to assess the correspondence between the variations in the chironomid assemblages and agricultural activity (Figure 6). The results of the DCA suggest that there is limited correspondence between faunal turnover and the changes in catchment vegetation during the late-Holocene. Although not definitive, the DCA does provide additional support that fluctuations in temperature are the main driver of chironomid community composition rather than agriculture-related nutrient enrichment.

The chironomid assemblages present at the base of the Laguna Zoncho profile, which are relatively depauperate, are dominated by taxa typically associated with warm, productive lakes found at middle and low elevations today (Wu et al., 2015). The presence of *Labrundinia* together with lower amounts of *Beardius* type A and *Dicrotendipes* in LZ-1 is suggestive of the presence of aquatic macrophytes. It is important to note that only three chironomid assemblages are available in LZ-1; therefore, the observed variations in the sub-fossil chironomid assemblages may not capture full range of environmental change during this interval. Zone LZ-1 corresponds to pollen zone 5 in the pollen, microscopic charcoal and stable carbon isotope records developed by Clement and Horn (2001) and Lane et al. (2004). The presence of maize pollen together with high percentages of Poaceae pollen, low tree pollen percentages, enriched sedimentary ^{13}C values, and high charcoal concentrations and charcoal:pollen ratios indicates an early interval of forest clearance and maize agriculture at Laguna Zoncho that began no later than the time of lake formation. From the chironomids, we can infer relatively warm conditions from ~3220–2740 cal. yr BP (Figure 6) during this initial agricultural period.

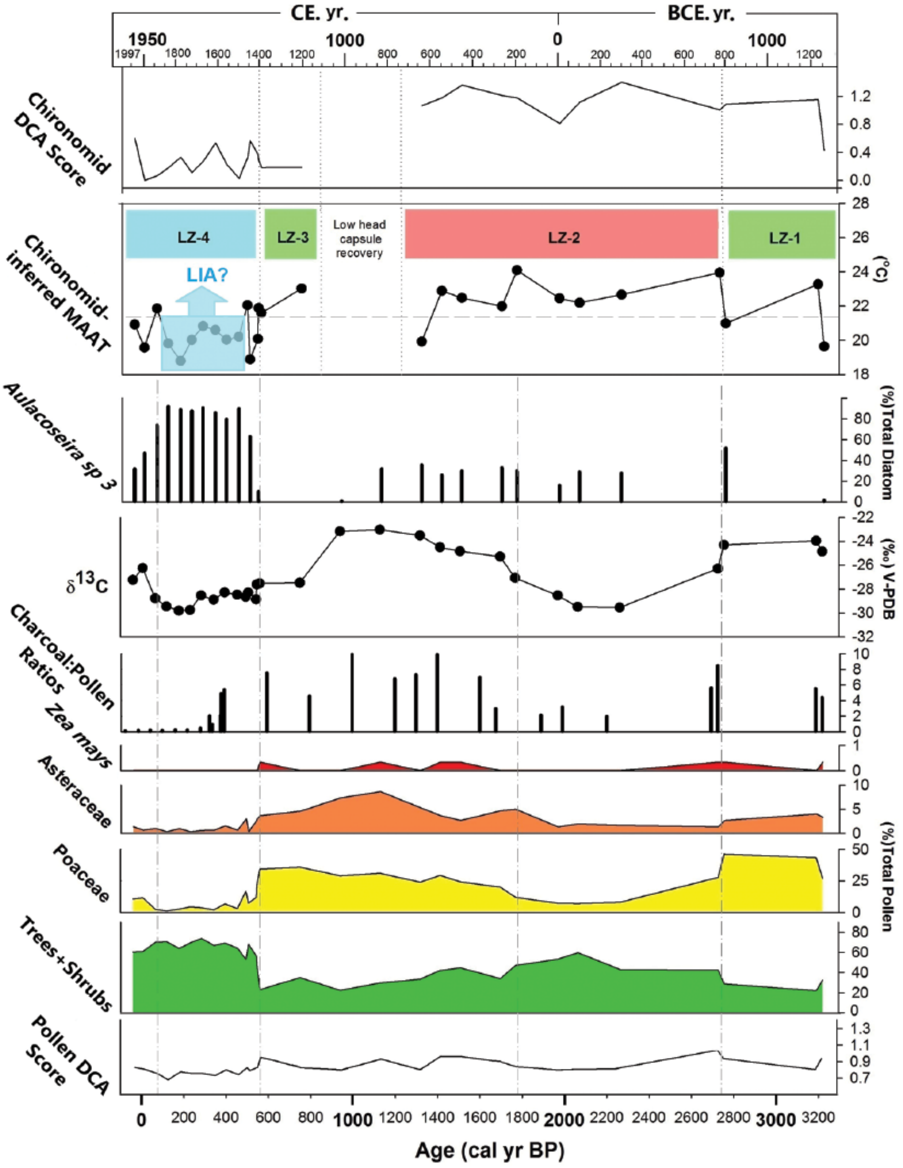

Figure 6. Summary diagram depicting pollen DCA scores, pollen abundance for select taxa, charcoal:pollen ratio, $\delta^{13}C$ values, the abundance of diatom taxon *Aulacoseira sp. 3*, and the chironomid-inferred MAAT reconstruction along with DCA first axis score (Clement and Horn, 2001; Haberyan and Horn, 2005; Lane et al., 2004; modified by Wu). Gray dotted lines indicate the chironomid zones. The gray dashed lines indicate the zonation based on diatom, pollen, and charcoal analyses, used in Clement and Horn (2001), Haberyan and Horn (2005), and Lane et al. (2004).

LZ-2 zone (~2740–1220 cal. yr BP or 790 BCE–730 CE; 271.5–176 cm) is characterized by an abrupt increase in chironomid richness. The increase in chironomid community diversity is driven by thermophilous taxa such as *Dicrotendipes, Polypedilum* type N, *Micropsectra*, and *Tanytarsus* type N. The presence of *Polypedilum* and *Microtendipes*, taxa inhabiting littoral and sublittoral sediments, together with the presence of thermophilous taxa and taxa associated with submerged vegetation indicate that this interval was characterized by higher temperatures, increased lake productivity, and the expansion of littoral habitat. This interpretation is supported by the quantitative chironomid-based reconstruction, which indicates the existence of elevated MAAT from ~2740 to 1220 cal. yr BP. The low sampling resolution in the basal portion of the LZ-2 precludes our ability to make definitive conclusions about the nature of the environmental change from 2740 to 1220 cal. yr BP. Changes in the diatom flora reveal that lower lake depth and more acidic lake water characterized Laguna Zoncho during this interval (Haberyan and Horn, 2005). The pollen record suggests that the catchment surrounding Laguna Zoncho experienced forest regrowth during the lower portion of LZ-2 (corresponding to pollen zone 4), followed by increased maize cultivation, forest clearance, and fire beginning ~1700 cal. yr BP (pollen zone 3) (Clement and Horn, 2001; Lane et al., 2004; Figure 6). The lower $\delta^{13}C$ values in LZ-2 likely reflect increased C_3 vegetation in the catchment resulting from reforestation (Lane et al., 2004).

The extremely low head capsule recovery that characterizes the chironomid stratigraphy from 176 to 144 cm (~1220–840 cal. yr BP or 730–1110 CE) likely reflects marked changes in limnological conditions at Laguna Zoncho. The near absence of chironomids during this interval could be explained by anthropogenic activities, climate change, or some combination of the influences of both climate change and anthropogenic disturbance. The pollen, charcoal, and stable carbon isotope records from the 1997 Zoncho core show evidence of increased intensity of maize cultivation during part of the interval of low chironomid productivity; this evidence includes the most enriched ^{13}C values, highest charcoal:pollen ratios, and the highest percentages of Asteraceae and Amaranthaceae pollen, interpreted as agricultural weeds, in the profile. Increased maize cultivation and burning may have led to increased erosion and sediment input to the lake, which in turn may have altered habitat and food availability for the chironomids. This inference is supported by the presence of *Rheotanytarsus*, albeit at low numbers, during this time. Increased erosion in the catchment would have facilitated the construction of larval cases consisting of coarser sediment such as sand by *Rheotanytarsus* (Pinder and Reiss, 1983).

Alternatively, it is possible that a decrease in effective moisture between ~1220 and 840 cal. yr BP lowered lake level to the point that only a limited pool of standing water remained at the core site, which would have decreased the chironomid diversity and abundance. This interval of low head capsule recovery may be linked to the impact of the Terminal Classic Drought (TCD), which consisted of a series of multi-decadal droughts that affected Central and South America and the Caribbean between 1200 and 850 cal. yr BP (750 and 1100 CE) (Lane et al., 2014) and may have contributed to the disintegration of the classic Maya civilization (Haug et al., 2003; Hodell et al., 2005a) as well as to cultural and environmental change throughout the circum-Caribbean region (Lane et al., 2009, 2011b, 2014). That the interval of low chironomid productivity at Laguna Zoncho may have been associated with a climate-mediated lowering of lake level is supported by high-resolution δ^{13}C records (Taylor et al., 2013a, 2015) of five sediment cores recovered from Laguna Zoncho in 2007. These analyses, carried out at much higher resolution than our chironomid, pollen, or prior isotope analyses, revealed two periods of basin-wide depletion of ^{13}C inputs interpreted to indicate agricultural decline associated with droughts from 1150 to 970 cal. yr BP (800–980 CE) and 860 to 640 cal. yr BP (1090–1310 CE). Finally, additional evidence of dry climate and lowered lake level in Costa Rica at this time is provided by lenses of macroscopic charcoals deposited at ~1100 cal. yr BP (850 CE) at Laguna Gamboa located 4 km southwest of Laguna Zoncho (Horn, 2007 and unpublished) and at Lago Chirripó in the Cordillera de Talamanca (Horn, 1993). Given the additional evidence of droughts at Laguna Zoncho and other sites in Costa Rica and the wider circum-Caribbean at this time, we find it reasonable to interpret the interval of low chironomid productivity in our record to reflect at least in part the influence of the TCD on hydroclimatology in Costa Rica; anthropogenic activities in the watershed may have also contributed.

In LZ-3 (~840–550 cal. yr BP or 1110–1400 CE), the diversity of the chironomid assemblage is reduced relative to LZ-2. The decrease in taxon richness is largely driven by the local extirpation of a number of taxa typically associated with warm, low-elevation lakes, for example, *Tanytarsus* type P and *Tanytarsus* type N (Wu et al., 2015). The notable increase in *Beardius* and the appearance of *Stenochironomus* likely reflect an expansion of aquatic macrophytes cover, the continued existence of relatively low lake levels, and elevated lake productivity (Cranston, 2010). The diatom flora in this zone is also very diverse, with an increase in *Eunotia minor* and the absence of *Aulacoseira sp. 3*, a planktonic diatom taxon; these aspects of the diatom assemblage together with relatively high values for the shallow water ratios of phytoliths:diatoms and sponge spicules:diatoms support the chironomid-based inference of lower lake level during this interval (Haberyan and Horn, 2005). Clement and Horn (2001) interpreted this time period in the upper part of pollen zone 3 as one of continued maize cultivation and agricultural burning, as shown by pollen and microscopic charcoal indices, but Taylor et al. (2013a, 2015) found evidence of declining ^{13}C ratios between 840 and 560 cal. yr BP in five cores collected from Laguna Zoncho in 2007 and interpreted these isotope shifts to indicate a period of population and agricultural decline in the watershed prior to the Spanish Conquest. Earlier analyses of stable carbon isotopes in the 1997 profile had also shown a drop in ^{13}C ratios within pollen zone 3, but the possible significance of this drop as an indicator of agricultural decline was not recognized. The interpretation of this agricultural decline as resulting from drought is consistent with the interpretation from the chironomid stratigraphy of low lake level.

Zone LZ-4 (~550– (−47) cal. yr BP or ~1400–1997 CE) is characterized by an increase in the relative abundance of taxa associated with relatively cold, high-elevation lakes such as *Procladius* and a decrease in taxa typically found in warm, productive low-elevation lakes such as *Paratanytarsus, Polypedilum* type N, and *Cladotanytarsus* (Figure 2). Today in Costa Rica, *Procladius* dominates high-elevation, glacial lakes (e.g. Lake Morrenas 0, 1, 2, 3, 4; Lago Chirripó; and Lago Ditkebi) and *Cricotopus* is mainly found in deep glacial lakes (Wu et al., 2015). The reduction of many littoral taxa, together with the increase in *Procladius* and *Cricotopus*, appears to indicate the onset of colder, less productive conditions at Laguna Zoncho. The shift in the chironomid assemblages in LZ-4 could reflect an increase in lake depth; however, based on autecological information and the lack of a statistically significant relationship between chironomid distributions and depth in the modern calibration set (Wu et al., 2015), we believe that the LZ-4 assemblages are reflective of a lowering of air temperature. The average chironomid-inferred MAAT declines to 20.3°C during LZ-4 period, which is 1.0°C lower than the late-Holocene chironomid-inferred MAAT average of 21.3°C. Additionally, notable excursions in MAAT occur at 1410 CE (18.9°C) and 1770 CE (18.8°C) (Figures 4 and 6). The existence of depressed MAAT (1.3°C lower than the 3200-year average) between 1480 CE and 1860 CE (470–90 cal. yr BP) may reflect the manifestation of the 'Little Ice Age' (LIA) in southern Costa Rica. Evidence of low-latitude cooling and drought during the 'LIA' has been documented at several sites in the circum-Caribbean (Böhm et al., 2002; Glynn et al., 1983; Hodell et al., 2005b; Lane et al., 2009, 2011b; Taylor et al., 2013a, 2015; Watanabe et al., 2001; Winter et al., 2000) and from the tropical Andes, where ice cores suggest marked cooling between 1400 CE and 1900 CE (Thompson et al., 2006). Lake and marine records recovered from study sites in the southern hemisphere also indicate the occurrence of 'LIA' cooling (Polissar et al., 2006; Rabatel et al., 2008). High atmospheric aerosol concentrations, resulting from several large volcanic eruptions and sea-ice/ocean feedbacks (Crowley and Lowery, 2000; Mann et al., 2009; Miller et al., 2012), have been implicated as the drivers responsible for the 'LIA'. On the basis of chironomid assemblages, we suggest that the 'LIA' in southern Costa Rica was characterized by ~1.3°C depression in MAAT relative to the late-Holocene MAAT average (Figure 6).

The diatom, pollen, δ^{13}C, and charcoal records document that Laguna Zoncho and the surrounding catchment were characterized by increasing lake levels, regeneration of forest, reduced burning, and a marked decrease in human activities beginning at ~1450 CE (Clement and Horn, 2001; Haberyan and Horn, 2005; Lane et al., 2004) or earlier (Taylor et al., 2013b, 2015). The Spanish Conquest greatly reduced indigenous populations in Costa Rica, and changes in terrestrial proxies in the Zoncho record may have been driven largely by these population reductions. However, agricultural declines prior to the Conquest were likely associated with drought, and colder and drier conditions during the 'LIA' would have affected people and environments in southern Pacific Costa Rica as in other areas of circum-Caribbean (e.g., Hodell et al., 2005b; Lane et al., 2011b). Based on a compilation of charcoal records from across the Americas, Power et al. (2013) concluded that cooling during the 'LIA' played a greater role in reducing fire occurrence after 1500 CE on a *global to continental scale* than did the post-contact collapse of indigenous populations. We recognize and in no way mean to discount the large and devastating cultural and environmental changes associated with the Spanish Conquest in Costa Rica. However, based on the indications of 'LIA' cooling in our chironomid record, and following Lane et al. (2011b), we suggest that climate change coincident with the arrival of Europeans deserves more attention as a factor that affected local and regional ecosystems, environments, and potentially human activities in Costa Rica.

Conclusion

This study pioneers the use of sub-fossil chironomid analysis in developing qualitative inferences of environmental change and quantitative estimates of thermal variability in Central America. Distinct shifts in chironomid community composition were observed during the late-Holocene. The notable shift in chironomid community composition that occurred at ~550 cal. yr BP (~1400 CE), characterized by an increase in the relative abundance of *Procladius* and a decrease in *Polypedilum, Cladotanytarsus*, and *Paratanytarsus*, suggesting that Laguna Zoncho was likely characterized by cooler, less productive conditions between ~1480 CE and 1860 CE. The chironomid-inferred MAAT during this interval shows 1.3°C below the ~3200-year MAAT average, providing evidence for the regional manifestation of the 'LIA' in Costa Rica. The near absence of sub-fossil chironomid remains between ~1220 and 840 cal. yr BP (~730–1110 CE), which likely reflects changes in habitat availability due to lowered lake levels, may be associated with decreased effective moisture during the TCD. Anthropogenic activities in the catchment such as forest clearance and cultivation of maize during the TCD may have also contributed to low chironomid abundance. The development of temperature reconstructions for Costa Rica will benefit from additional analyses of chironomid stratigraphies, especially at sites of more limited human impact during the Holocene.

Acknowledgements

We thank the late Luis Diego Gómez for encouraging Sally P Horn to begin work at Laguna Zoncho, former land owner Michelle Cloud and current landowners Gail Hewson Hull and Harry Hull for permission for repeated sampling at the lake, Lisa Kennedy and Brandon League for assistance with sediment coring, and Professor Maureen Sánchez of the University of Costa Rica and the Organization for Tropical Studies for logistical support. We also thank Scott Reinemann, Xuebin Wei, and Yu Luo for providing comments on the manuscript.

Funding

A University of Georgia Provost's Summer Research Award and a University of Georgia SEC Visiting Faculty Travel Grant to David F Porinchu provided support for this research. Sediment coring at Laguna Zoncho and radiocarbon dates were funded by a grant to Sally P Horn and RL Sanford, Jr, from The A.W. Mellon Foundation, and core sampling for chironomids was supported by the Initiative for Quaternary Paleoclimate Research at the University of Tennessee.

References

Axford Y, Briner JP, Cooke CA et al. (2009) Recent changes in a remote Arctic lake are unique within the past 200,000 years. *Proceedings of the National Academy of Sciences of the United States of America* 106: 18443–18446.

Barley EM, Walker IR, Kurek J et al. (2006) A northwest North American training set: Distribution of freshwater midges in relation to air temperature and lake depth. *Journal of Paleolimnology* 36: 295–314.

Birks HJB (1998) DG Frey and ES Deevey review 1: Numerical tools in palaeolimnology progress, potentialities, and problems. *Journal of Paleolimnology* 20: 307–332.

Birks HJB, Line JM, Juggins S et al. (1990) Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London B. Series B, Biological Sciences* 327: 263–278.

Böhm F, Haase-Schramm A, Eisenhauer A et al. (2002) Evidence for preindustrial variations in the marine surface water carbonate system from coralline sponges. *Geochemistry, Geophysics, Geosystems* 3: 1–13.

Brooks SJ, Langdo PG and Heiri O (2007) The identification and use of palaearctic chironomidae larvae in palaeoecology. Quaternary Research Association Technical Guide 10. Available at: http://link.springer.com/article/10.1007%2Fs10933-007-9191-1.

Clement RM and Horn SP (2001) Pre-Columbian land-use history in Costa Rica: A 3000-yearrecord of forest clearance, agriculture and fires from Laguna Zoncho. *The Holocene* 11: 419–563.

Colinvaux PA, De Oliveira PE and Moreno JE (1999) *Amazon Pollen Manual and Atlas*. London; New York: Gordon and Breach (Hardwood), p. 310.

Cranston P (2010) Available at: http://chirokey.skullisland.info/.

Crowley TJ and Lowery TS (2000) How warm was the medieval warm period? *AMBIO: A Journal of the Human Environment* 29: 51–54.

Eggermont H, Heiri O, Russell J et al. (2010) Paleotemperature reconstruction in tropical Africa using fossil Chironomidae (Insecta: Diptera). *Journal of Paleolimnology* 43: 413–435.

Eggermont H, Kennedy D, Hasiotis ST et al. (2008) Distribution of living larval Chironomidae (Insecta: Diptera) along a depth transect at Kigoma Bay, Lake Tanganyika: Implications for palaeoenvironmental reconstruction. *African Entomology* 16: 162–184.

Engels S, Bohncke SJP, Bos JAA et al. (2008) Chironomid-based palaeotemperature estimates for northeast Finland during Oxygen Isotope Stage 3. *Journal of Paleolimnology* 40: 49–61.

Epler JH (1995) *Identification Manual for the Larval Chironomidae (Diptera) of Florida* (Revised Edition). Tallahassee, FL: Florida Department Environmental Protection, p. 317.

Epler JH (2001) *Identification Manual for the Larval Chironomidae (Diptera) of North and South Carolina: A Guide to the Taxonomy of the Midges of the Southeastern United States, Including Florida* (Special Publication SJ2001-SP13. North Carolina Department of Environment and Natural Resources). Palatka, FL: St. Johns River Water Management District, 526 pp.

Filippelli GM, Souch C, Horn SP et al. (2010) The pre-Colombian footprint on terrestrial nutrient cycling in Costa Rica: Insights from phosphorus in a lake sediment record. *Journal of Paleolimnology* 43: 843–856.

Glynn PW, Druffel EM and Dunbar RB (1983) A dead Central American coral reef tract: Possible link with the Little Ice Age. *Journal of Marine Research* 41: 605–637.

Haberyan KA and Horn SP (2005) Diatom paleoecology of Laguna Zoncho, Costa Rica. *Journal of Paleolimnology* 33: 361–369.

Haug GH, Günther D, Peterson LC et al. (2003) Climate and the collapse of Maya Civilization. *Science* 299: 1731–1735.

Heiri O, Brooks SJ, Birks HJB et al. (2011) A 274-lake calibration data-set and inference model for chironomid-based summer air temperature reconstruction in Europe. *Quaternary Science Reviews* 30: 3445–3456.

Heiri O, Lotter AF, Hausmann S et al. (2003) A chironomid-based Holocene summer air temperature reconstruction from the Swiss Alps. *The Holocene* 13: 477–484.

Hodell DA, Brenner M and Curtis JH (2000) Climate change in the northern America tropics and subtropics since the last ice age. In: Lentz DL (ed.) *Imperfect Balance: Landscape Transformations in the Precolumbian Americas*. New York: Columbia University Press, pp. 13–38.

Hodell DA, Brenner M and Curtis JH (2005a) Terminal Classic drought in the northern Maya lowlands inferred from multiple sediment cores in Lake Chichancanab (Mexico). *Quaternary Science Reviews* 24: 1413–1427.

Hodell DA, Brenner M, Curtis JH et al. (2005b) Climate change on the Yucatan Peninsula during the Little Ice Age. *Quaternary Research* 63: 109–121.

Hodell DA, Brenner M, Curtis JH et al. (2001) Solar forcing of drought frequency in the Maya lowlands. *Science* 292: 1366–1370.

Holdridge LR, Grenke WC, Hatheway WH et al. (1971) *Forest Environments in Tropical Life Zone System: A Pilot Study*. Oxford: Pergamon Press.

Hooghiemstra H, Cleef AM, Noldus CW et al. (1992) Upper Quaternary vegetation dynamics and palaeoclimatology of the La Chonta bog area (Cordillera de Talamanca, Costa Rica). *Journal of Quaternary Science* 7: 205–225.

Horn SP (1993) Postglacial vegetation and fire history of the Chirrup Paramo of Costa Rica. *Quaternary Research* 40: 107–116.

Horn SP (2007) Late Quaternary lake and swamp sediments: Records of climate and environment. In: Bundschuh J and Alvarado GE (eds) *Central America: Geology, Resources, and Hazards*, vol. 1. London: Taylor & Francis, pp. 423–441.

Horn SP and Haberyan KA (2016) Lakes of Costa Rica. In: Kappelle M (ed.) *Costa Rican Ecosystems*. Chicago, IL: University of Chicago Press, pp. 656–682.

Ilyashuk BP and Ilyashuk EA (2007) Chironomid record of Late Quaternary climatic and environmental changes from two sites in Central Asia (Tuva Republic, Russia) – Local, regional or global causes? *Quaternary Science Reviews* 26: 705–731.

Ilyashuk EA, Koing KA, Heiri O et al. (2011) Holocene temperature variations at a high-altitude site in the Eastern Alps: A chironomid record from Schwarzsee ob Sölden, Austria. *Quaternary Science Reviews* 30: 176–191.

Islebe GA, Hooghiemstra H and van't Veer R (1996) Holocene vegetation and water level history in two bogs of the Cordillera de Talamanca, Costa Rica. *Vegetatio* 124: 155–171.

Jacobsen RE and Perry SA (2000) A review of Beardius Reiss & Sublette, with description of a new species from Everglades National Park, Florida (Insecta, Diptera, Chironomidae). *Spixiana* 23: 129–144.

Juggins S (2003) *C2 User Guide: Software for Ecological and Palaeoecological Data Analysis and Visualisation*. Newcastle upon Tyne: University of Newcastle, p. 69.

Juggins S (2014) Analysis of quaternary science data. Available at: http://cran.rproject.org/web/packages/rioja/index.html.

Lachniet MS and Seltzer GO (2002) Late Quaternary glaciation of Costa Rica. *Geological Society of America Bulletin* 114: 547–558.

Lane CS and Horn SP (2013) Terrestrially derived n-Alkane δD evidence of shifting Holocene Paleohydrology in highland Costa Rica. *Arctic, Antarctic, and Alpine Research* 45:342–349.

Lane CS, Horn SP and Kerr MT (2014) Beyond the Mayan lowlands: Impacts of the terminal classic drought in the Caribbean Antilles. *Quaternary Science Reviews* 86: 89–98.

Lane CS, Horn SP and Mora CI (2004) Stable carbon isotope ratios in lake and swamp sediments as a proxy for prehistoric forest clearance and crop cultivation in the Neotropics. *Journal of Paleolimnology* 32: 375–381.

Lane CS, Horn SP, Mora CI et al. (2011a) Sedimentary stable carbon isotope evidence of late Quaternary vegetation and climate change in highland Costa Rica. *Journal of Paleolimnology* 45: 323–338.

Lane CS, Horn SP, Orvis KH et al. (2011b) Oxygen isotope evidence of Little Ice Age aridity on the Caribbean slope of the Cordillera Central, Dominican Republic. *Quaternary Research* 75: 461–470.

Lane CS, Horn SP, Taylor ZP et al. (2009) Assessing the scale of prehistoric human impact in the neotropics using stable carbon isotope analyses of lake sediments: A test case from Costa Rica. *Latin American Antiquity* 20:120–133.

League BL and Horn SP (2000) A 10000 year record of Páramo fires in Costa Rica. *Journal of Tropical Ecology* 16: 747–752.

Levesque AJ, Cwynar LC and Walker IR (1997) Exceptionally steep north-south gradients in lake temperatures during the last deglaciation. *Nature* 385:423–426.

Mann ME, Zhang ZH, Rutherford S et al. (2009) Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science* 326: 1256–1260.

Massaferro JI, Moreno PI, Denton GH et al. (2009) Chironomid and pollen evidence for climate fluctuations during the Last Glacial Termination in NW Patagonia. *Quaternary Science Reviews* 28: 517–525.

Miller GH, Geirsdóttir A, Zhong YF et al. (2012) Abrupt onset of the Little Ice Age triggered by volcanism and sustained by sea-ice/ocean feedbacks. *Geophysical Research Letters* 39. Available at: http://onlinelibrary.wiley.com/doi/10.1029/2011GL050168/abstract.

Ortiz E (2005) *Atlas Digital de Costa Rica 2004*. Cartago, Costa Rica: Instituto Tecnológico de Costa Rica, Escuela de Ingeniería Forestal. Available at: http://ots.ac.cr/index.php?option=com_wrapper&;Itemid=427.

Orvis KH and Horn SP (2000) Quaternary glaciers and climate on Cerro Chirripó, Costa Rica. *Quaternary Research* 54: 24–37.

Pinder LCV and Reiss F (1983) The larvae of Chironominae (Diptera: Chironomidae) of the Holartic region – Keys and diagnoses. In: Wiederholm T (ed.) *Chironomidae of the Holartic Region: Keys and Diagnoses: Larvae*, part 1 (Entomologica Scandinavica, supplement 19). Motala: Borgströms Tryckeri AB, pp. 293–435.

Polissar PJ, Abbott M, Wolfe AP et al. (2006) Solar modulation of Little Ice Age climate in the tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America* 103: 8937–8942.

Porinchu DF and MacDonald GM (2003) The use and application of freshwater midges (Chironomidae: Insecta: Diptera) in geographical research. *Progress in Physical Geography* 27: 378–422.

Porinchu DF, Reinemann SA, Mark BG et al. (2010) Application of a midge-based inference model for air temperature reveals evidence of late-20th century warming in sub-alpine lakes in the central Great Basin, United States. *Quaternary International* 215: 15–26.

Power MJ, Mayle FE, Bartlein PJ et al. (2013) Climate control of the biomass-burning decline in the Americas after AD 1500. *The Holocene* 23: 3–13.

Rabatel A, Francou B, Jomelli V et al. (2008) A chronology of the Little Ice Age in the tropical Andes of Bolivia (16°S) and its implications for climatic reconstruction. *Quaternary Research* 70: 198–212.

Reimer PJ, Bard E, Bayliss A et al. (2013) IntCal13 and marine 13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55: 1869–1887.

Reinemann SA, Porinchu DF, Bloom AM et al. (2009) A multiproxy paleolimnological reconstruction of Holocene climate conditions in the Great Basin, United States. *Quaternary Research* 72: 347–358.

Reinemann SA, Porinchu DF, MacDonald GM et al. (2014) A 2000-yr reconstruction of air temperature in the Great Basin of the United States with specific reference to the Medieval Climatic Anomaly. *Quaternary Research* 82:309–317.

Self EA, Brooks SJ, Birks HJB et al. (2011) The distribution and abundance of chironomids in high-latitude Eurasian lakes with respect to temperature and continentality: Development and application of new chironomid-based climate-inference models in northern Russia. *Quaternary Science Reviews* 30: 1122–1141.

Taylor ZP, Horn SP and Finkelstein DB (2013a) Maize pollen concentrations in Neotropical lake sediments as an indicator of the scale of prehistoric agriculture. *The Holocene* 23: 78–84.

Taylor ZP, Horn SP and Finkelstein DB (2013b) Prehispanic agricultural decline prior to the Spanish conquest in southern Central America. *Quaternary Science Reviews* 73: 196–200.

Taylor ZP, Horn SP and Finkelstein DB (2015) Assessing intra-basin spatial variability in geochemical and isotopic signatures in the sediments of a small neotropical lake. *Journal of Paleolimnology* 54: 395–411.

Thompson LG, Thompson EM, Brecher H et al. (2006) Abruption tropical climate change: Past and present. *Proceedings of the National Academy of Sciences of the United States of America* 103: 10536–10543.

Walker IR (2001) Midges: Chironomidae and related Diptera. In: Smol JP, Birks HJB and Last WM (eds) *Tracking Environmental Change Using Lake Sediments: Zoological Indicators – Developments in Paleoenvironmental Research*, vol. 4. Dordrecht: Kluwer, pp. 43–66.

Walker IR and Cwynar LC (2006) Midges and palaeotemperature reconstruction – The North American experience. *Quaternary Science Reviews* 25: 1911–1925.

Watanabe T, Winter A and Oba T (2001) Seasonal changes in sea surface temperature and salinity during the Little Ice Age in the Caribbean Sea deduced from Mg/Ca and^{18}O/^{16}O ratios in corals. *Marine Geology* 173: 21–35.

Winter A, Oba T, Ishioroshi H et al. (2000) Tropical sea surface temperatures: Two-to-three degrees cooler than present during the Little Ice Age. *Geophysical Research Letters* 27: 3365–3368.

Wu JY, Porinchu DF, Horn SP et al. (2015) The modern distribution of chironomid sub-fossils (Insecta: Diptera) in Costa Rica and the development of a regional chironomid-based temperature inference model. *Hydrobiologia* 742: 107–127.