

# The modern distribution of chironomid sub-fossils (Insecta: Diptera) in Costa Rica and the development of a regional chironomid-based temperature inference model

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**Abstract** Chironomids have been shown to provide robust reconstructions of past temperature change and variability. This is the first study to assess the contemporaneous relationship between the distribution of sub-fossil chironomids and limnological and climatic parameters in Central America. Here, we describe the distribution of chironomids in a suite of 51 lakes in Costa Rica. We identify environmental variables that account for a statistically significant amount of variance in midge distribution, and develop a quantitative chironomid-based inference model for mean annual air temperature (MAT). *Psectrocladius*, which is documented for the first time in Costa Rica, dominate high-elevation lakes characterized by low MAT and relatively dilute water. Canonical correspondence analysis (CCA) revealed that MAT and conductivity account for large, statistically significant amounts of variance in the distribution of

chironomids. A chironomid-based inference model for MAT, developed using a partial least squares approach, provided robust performance statistics with a high coefficient of determination and a relatively low root-mean square error. Application of the chironomid-based inference model for MAT to chironomid stratigraphies spanning the Holocene, together with the ecological information provided by this study, will enable us to address many outstanding questions relating to long-term climate and environmental change in the region.

**Keywords** Paleoclimate · Transfer function · Chironomid · Costa Rica · Paleolimnology · Mean annual air temperature

## Introduction

The sediments of lakes and bogs in Costa Rica have been a focus of intensive paleoclimate and paleoenvironmental research, with numerous multi-proxy studies undertaken in recent decades (e.g., Islebe & Hooghiemstra, 1997; Lane et al., 2009a; Lane & Horn, 2013; Taylor et al., 2013). The results from these studies have provided valuable insights into the nature of tropical climate and landscape change during the late Pleistocene and Holocene for this region. For example, much of what is known about late Holocene climate and environmental change in southern Costa Rica comes from detailed analyses of lake sediment cores recovered from Laguna Zoncho (Clement &

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Horn, 2001; Lane et al., 2004; Haberyan & Horn, 2005; Filippelli et al., 2010; Taylor et al., 2013). Clement & Horn (2001) analyzed the pollen and charcoal in a core from the center of Laguna Zoncho and developed a 3,000-year record of indigenous settlement, forest clearance, maize cultivation, and fire. This study also constrained the timing of the earliest cultivation of maize (*Zea mays* subsp. *mays*) in southern Costa Rica (Horn, 2006). A network of six cores was later recovered from the same lake to develop a spatially explicit, high-resolution record of human activity and climate change for the Laguna Zoncho basin (Taylor et al., 2013). Analyses of stable carbon isotopes, geochemistry, and diatoms in Zoncho lake sediments provide additional evidence of periods of decreased effective moisture during the late Holocene. The inferred changes in local hydroclimate, the timing of which correspond to other sites in the circum-Caribbean (Haug et al., 2001, 2003; Lane et al. 2009b, 2011, 2014), may be driven by shifts in the mean position of the Intertropical Convergence Zone (ITCZ) (Taylor et al., 2013).

Although numerous proxy-based reconstructions describing various aspects of late Holocene environmental change have been developed for Costa Rica, the degree to which thermal conditions contributed to observed landscape and limnological change remains poorly described. In studies of lake sediments, subfossil chironomids have been proven to provide robust reconstructions of past temperature change and variability (Porinchi & MacDonald, 2003; Walker & Cwynar, 2006; Brooks, 2006). Previous studies have provided evidence that variations in chironomid assemblages are strongly correlated to temperature (air and water) in North America (Walker et al., 1991a, b; Walker & MacDonald, 1995; Barley et al., 2006; Larocque et al., 2006; Porinchi et al., 2007, 2009, 2010), Europe (Olander et al., 1999; Korhola, 1999; Brooks & Birks, 2001; Heiri et al., 2003; Heiri & Millet, 2005; Luoto, 2009; Heiri et al., 2011), Eurasia (Brooks, 2006; Self et al., 2011), Africa (Eggermont et al., 2010), Australasia (Dieffenbacher-Krall et al., 2007; Rees et al., 2008; Rees & Cwynar, 2010), and South America (Massaferro & Brooks, 2002; Massaferro & Larocque-Tobler, 2013). Chironomids are sensitive indicators of past temperature and offer great potential to provide independent estimates of regional climate conditions during intervals of transition (Cwynar & Levesque, 1995; Porinchi & Cwynar,

2002; Porinchi et al., 2003; Engels et al., 2008; Brooks & Heiri, 2013). However, only one study using sub-fossil chironomid analysis has been undertaken in Central America (Pérez et al., 2010), and none to date in Costa Rica. Describing and determining the distribution and the environmental optima and tolerances of chironomid taxa in relation to the contemporaneous environment will improve our ability to interpret down core variations in sub-fossil chironomid communities, which in turn will help shed additional light on late Quaternary climate change in Costa Rica.

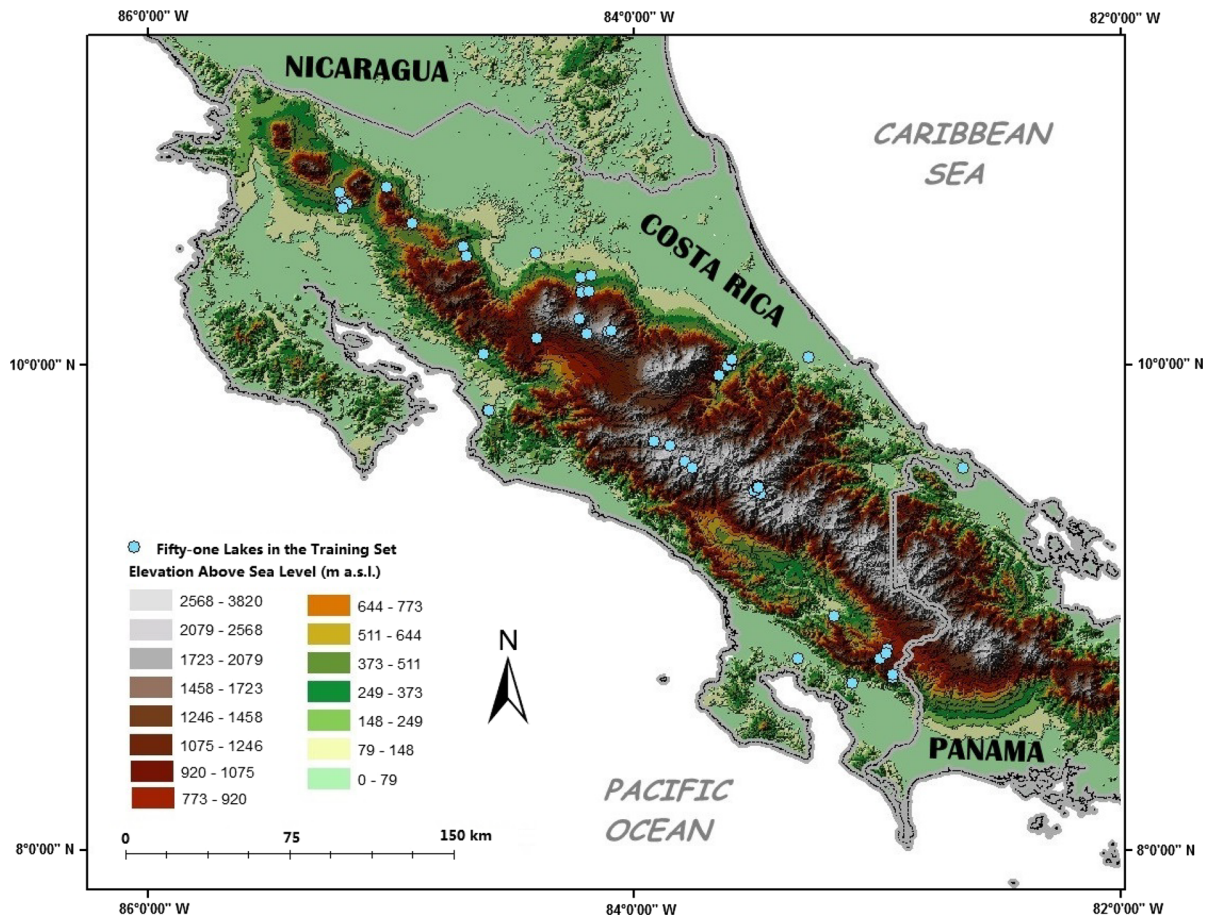
In this study, we sought to qualitatively and quantitatively describe the modern distribution of sub-fossil chironomids in a suite of 51 lakes in Costa Rica. The primary goal of the study was to develop a chironomid-based inference model for application to the subfossil assemblages in sediment profiles from Costa Rican lakes, to provide quantitative estimates of past environmental conditions.

## Materials and methods

### Study area

Costa Rica, located in the narrow southern portion of the Central American isthmus, is characterized by a central mountainous spine composed of a series of northwest–southeast trending mountain ranges (Fig. 1). The northern ranges begin near the Nicaraguan border with the volcanic Cordillera de Guanacaste, and extend southeastward through the Cordillera de Tilarán to the high volcanoes of the Cordillera Central, on the northern edge of the populous Meseta Central. These ranges include more than a dozen Quaternary stratovolcanoes, nine of which are still active (Van Wyk De Vries et al., 2007; Bundschuh et al., 2007). The rugged Cordillera de Talamanca, a plutonic mountain range, rises to the south and east of the Meseta Central and extends beyond the border with Panama. This mountain range, high enough to have been glaciated during the Pleistocene (Orvis & Horn, 2000; Lachniet & Seltzer, 2002), consists principally of uplifted Tertiary volcanic and sedimentary rocks, with a granitic core.

The climate of Costa Rica is tropical, with low seasonal variation in temperature but marked seasonality of precipitation, especially in the central highlands and Pacific lowlands. Distinct wet and dry



**Fig. 1** Location of the 51 lakes in the Costa Rican chironomid calibration set. Lakes are marked by *blue dots*. DEM data for Costa Rica is from the geocommunity database, <http://data.geocomm.com/catalog/CS/group121.html>

seasons are produced by the shift in the position of equatorial low pressure and subtropical high pressure over Central America in response to the seasonal migration of the sub-solar point and ITCZ (Bundschuh et al., 2007). For most of the Pacific slope the wet season begins in May when the ITCZ shifts northward, and ends in November when the ITCZ migrates southward (Coen, 1983). Rainfall in the Caribbean lowlands is highest in December and January, associated with the intensification of the northern hemisphere polar front (Coen, 1983; Bundschuh et al., 2007).

The location of Costa Rica within the equatorial tropics (latitudinal range 8°N to 11°N) results in temperature patterns characterized by only small differences between mean monthly temperature in January (MMJT) and July (AJUMT). Temperature

declines with increasing elevation, with MMJT ranging from 26.0°C in the lowlands to an estimated 6.25°C at 3,819 m above sea level (a.s.l.) on Cerro Chirripó in the Cordillera de Talamanca, the highest point in the country (Bundschuh et al., 2007). The amount and spatial distribution of precipitation is also strongly influenced by topography (Coen, 1983; Clawson, 1997; Bundschuh et al., 2007). Annual rainfall totals range from 1,500 to 2,000 mm in the northwest Pacific lowlands, which are dominated by seasonal dry forests and savannas, to 3,000–4,000 mm or more on the windswept Caribbean slope of the Cordillera de Talamanca, which supports evergreen moist and cloud forests (Coen, 1983; Horn & Haberyan, 1993, *in press*; George et al., 1998; Bundschuh et al., 2007; Kappelle, 2014/2015). Precipitation is somewhat lower on the highest peaks of the Cordillera

de Talamanca, which support grass- and shrub-dominated páramo vegetation (Kappelle & Horn, 2005).

High annual rainfall, a wide array of basin forming geomorphic processes, and human activity have created over 600 water bodies in Costa Rica (Horn & Haberyan, *in press*). These water bodies are distributed throughout the country from sea level to the highest peaks. The calibration dataset includes oxbow lakes, wetland lakes, artificial lakes (reservoirs and farm ponds), lava- and lahar-dammed lakes, landslide lakes, crater lakes, and glacial lakes (Haberyan et al., 2003). The physical and chemical limnology of the calibration set lakes, which is a function of ontogeny and location, varies greatly (Horn & Haberyan, 1993; Haberyan et al., 2003). The 51 lakes (Fig. 1) in the training set for this paper include 38 natural lakes formed through volcanic, fluvial, glacial, or mass wasting processes, and 13 lakes formed from artificial impoundments (Horn & Haberyan, 1993; Haberyan et al., 2003). They are located in seven ecosystem regions (Horn & Haberyan, *in press*). The northern highland evergreen moist forest, southern highland evergreen cloud forest, the southern highland páramo grassland, and the northern Pacific lowland deciduous dry forest contain the greatest number of lakes in this study, with 13, 11, 10 and 7 lakes, respectively. The rest of the lakes are located in the Caribbean lowland evergreen moist forest, southern Pacific lowland evergreen moist forest, or Nicoya-Tempisque Pacific dry forest.

#### Field and laboratory methods

Surface sediment, water samples, and limnological data were collected from 51 lakes in Costa Rica (Fig. 1). Most of the sediment samples and limnological data, described in greater detail in Horn & Haberyan (1993) and Haberyan et al. (2003), were collected in July 1991 and July 1997, with additional limnological measurements and collections made in March 1998, March 1999, March 2000, and March 2001. Water samples were typically collected near the center of the lakes. Basic geographic information, including names, locations, elevations, and surface area of the 51 lakes (Table 1) was determined using the 1:50,000 scale topographic maps published by the Instituto Geográfico Nacional de Costa Rica.

Oxygen, pH, and conductivity were measured using YSI model 54, Oakton pH, and Hanna HI 8,733 m, and

transparency was measured using a Secchi disk. Carbon dioxide was analyzed immediately following sample collection and alkalinity was measured within 5 h, using LaMotte test kits. Water samples collected in 1991 and 1997 were filtered, while those obtained in 1998, 1999, and 2003 were not. Sealed samples were returned for additional chemical analyses, including concentration of  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{K}^+$ ,  $\text{Na}^+$ ,  $\text{Si}$ , and  $\text{Cl}^-$  (Table 1) (see Horn & Haberyan, 1993; Haberyan et al., 2003 for additional details).

We used mean annual air temperature (MAT) as the estimate of temperature in the direct gradient analyses. For stations at all elevations in Costa Rica the difference in mean temperature between the warmest and coolest month is  $<5^\circ\text{C}$  (Coen, 1983), making MAT an appropriate variable. The estimates of MAT for the lakes in the training set were calculated from the surface lapse rate provided in Orvis & Horn (2000). Based on historical air temperature records from 188 Costa Rica meteorological stations, Orvis & Horn (2000) derived a mean annual surface lapse rate of  $5.42^\circ\text{C}/\text{km}$  and a mean annual base temperature at sea level of  $26.6 \pm 1.3^\circ\text{C}$ . The MAT for each of the 51 lakes in the training set (Table 1) was determined using the following equation:

$$\text{MAT} = 26.6^\circ\text{C} - [\text{Elevation (m a.s.l.)} \\ \times 0.00542^\circ\text{C}/\text{m}].$$

#### Laboratory analyses

Chironomid samples were analyzed following standard procedures as outlined in Walker (2001). The sediment was treated with 5% KOH solution to facilitate the break-up of colloidal matter. A known volume (usually 0.5–22.0 ml) of wet sediment was placed in a beaker with 50 ml of 5% KOH and heated at  $50^\circ\text{C}$  for approximately 30 min. The deflocculated sediment was washed through a  $95\ \mu\text{m}$  mesh using distilled water and the material retained on the mesh was backwashed into the beaker. A dissection microscope at  $50\times$  and a Bogorov plankton counting tray were used to separate the chironomid head capsules from the sediment matrix. The chironomid remains were permanently mounted on slides in Entellan<sup>®</sup> for identification. Taxonomic identification was done at  $400\times$ , typically to genus, relying primarily on larval keys for Florida and North and South Carolina (Epler, 1995, 2001), with Brooks et al. (2007), Eggermont

**Table 1** Geographic and limnological data for the 51 lakes in the Costa Rican calibration set

Lake name	Lake code	Sample code	Eco reg	Lat (°N)	Lon (°W)	Ele (m)	Depth (m)	MAT (°C)	pH	Conduct (µS cm <sup>-1</sup> )	O <sub>2</sub> (mg l <sup>-1</sup> )	CO <sub>2</sub> (mg l <sup>-1</sup> )	Alk (mg l <sup>-1</sup> )	Ca <sup>2+</sup> (mg l <sup>-1</sup> )	Mg <sup>2+</sup> (mg l <sup>-1</sup> )	K <sup>+</sup> (mg l <sup>-1</sup> )	Na <sup>+</sup> (mg l <sup>-1</sup> )	Si (mg l <sup>-1</sup> )	Cl <sup>-</sup> (mg l <sup>-1</sup> )
Quebrador	1	9107	6	9.603	83.790	3,040	2.0	10.1	6.7	0	6.4	4	23	2.14	0.42	0.00	2.90	9.05	1.48
Cañon	2	9108	6	9.685	83.916	2,480	1.3	13.2	5.6	0	4.1	6	5	7.83	0.61	1.07	1.51	1.85	2.61
Tres de Junio	3	9707	6	9.666	83.851	2,670	0.7	12.1	5.2	30	5.8	12	3	1.68	0.33	5.20	7.28	0.36	9.38
Asunción	4	9107	6	9.575	83.759	3,340	1.0	8.5	4.9	0	6.9	3	0	0.76	0.17	1.13	3.00	0.72	9.43
Chirripó 1	5	0003	7	9.484	83.498	3,520	22.0	7.5	5.4	0	5.2	3	8	1.23	0.17	0.00	0.81	0.93	0.42
Morrenas1	6	9802	7	9.494	83.489	3,477	8.3	7.8	7.3	0	6.6	3	10	1.86	0.20	0.57	1.37	1.84	1.27
Cote	8	9107	5	10.583	84.913	650	11.0	23.1	7.2	20	8.3	3	26	2.38	0.94	1.21	3.85	4.62	7.55
Botos	10	9107	5	10.188	84.225	2,600	5.0	12.5	4.4	30	7.3	6	1	2.68	0.60	2.50	2.20	2.40	6.51
Barva	11	9903	5	10.135	84.107	2,840	7.9	11.2	7.5	60	8.0	4	9	0.63	0.32	1.39	7.41	0.84	9.49
Fraijanes	12	9107	5	10.127	84.193	1,650	6.2	17.7	7.3	90	8.8	4	69	8.51	3.84	4.35	8.17	7.96	9.51
Serafin	16	9108	5	10.111	84.399	1,140	0.7	20.4	6.7	100	6.2	15	100	12.91	3.94	1.78	5.13	26.91	3.39
Congo	20	9107	5	10.306	84.216	740	14.6	22.6	6.5	60	6.8	3	3	0.91	0.26	0.00	0.94	2.80	9.52
Bosque Alegre	21	9107	6	10.299	84.217	740	4.0	22.6	6.4	60	10.4	0	11	6.70	1.71	0.90	5.05	12.71	8.66
María Aguilar	22	9107	6	10.302	84.187	770	6.9	22.4	5.7	60	6.0	6	12	4.68	1.14	1.71	4.24	7.57	9.14
Santa Isabel	24	9107	3	10.369	84.177	160	3.0	25.7	6.4	20	6.7	5	12	1.51	0.50	0.98	3.96	3.66	9.54
Bonilla	25	9107	3	9.994	83.604	380	27.0	24.5	7.0	139	6.7	4	97	8.60	5.16	2.84	4.90	16.45	1.70
Bonillita	26	9107	3	9.993	83.614	450	20.0	24.2	7.0	19	5.8	5	23	2.36	1.16	1.13	2.10	3.78	1.60
Azul	27	9107	5	9.956	83.652	630	2.0	23.2	7.2	240	6.7	13	174	18.96	3.94	5.24	31.70	4.82	9.44
La Palma	31	9707	5	10.488	84.702	570	10.8	23.5	8.2	293	11.3	6	130	21.64	17.21	2.82	15.02	25.53	10.68
Lancaster Arriba	36	9402	3	10.023	83.598	430	2.0	24.3	6.9	108	4.8	21	64	8.25	4.13	1.60	6.28	15.45	2.69
Cocoritos	38	9707	5	10.043	84.618	520	1.0	23.8	7.4	114	7.8	6	19	1.76	0.74	0.86	2.46	5.42	2.60
Cerro Chato	39	9707	5	10.444	84.689	1,050	17.9	20.9	7.2	28	7.0	3	8	0.32	0.12	0.00	1.15	0.27	2.00
San Francisco	40	9707	5	10.458	84.405	90	2.5	26.1	8.0	144	6.8	6	72	10.76	5.00	1.60	6.51	21.98	3.50
Osa 1	42	9707	4	8.684	83.505	30	1.5	26.4	7.1	40	6.5	5	22	0.71	0.53	3.08	0.73	2.28	1.40
Sierpe	43	9707	4	8.789	83.327	16	2.2	26.5	7.1	102	6.6	6	48	8.88	3.50	0.00	4.40	9.90	2.60
Foster	44	9707	4	8.690	83.102	40	1.5	26.4	7.8	89	9.1	6	159	53.83	2.43	0.00	4.87	11.61	0.70
Campo Dos	45	9707	6	8.710	82.937	1,036	1.5	21.0	7.0	54	6.5	9	39	5.69	0.94	0.00	1.64	6.31	0.30
Campo Tres	46	9707	6	8.723	82.935	1,097	2.6	20.7	7.0	44	4.6	10	31	4.20	0.70	0.00	1.00	4.50	0.40
Gambosa	47	9707	6	8.788	82.988	1,460	2.0	18.7	6.9	17	2.8	14	16	0.64	0.29	0.00	0.57	0.86	0.40
San Joaquín	48	9707	6	8.830	82.958	976	1.0	21.3	6.3	41	4.2	17	26	3.90	1.31	0.00	1.47	4.87	0.70
Zoncho	50	9707	6	8.813	82.963	1,190	2.6	20.2	7.4	16	7.1	3	12	0.66	0.20	0.00	0.84	0.69	0.10
Vueltas	51	9707	4	8.967	83.178	270	3.0	25.1	8.7	233	10.1	0	125	21.72	8.43	3.86	7.02	20.95	1.50
San Miguel	56	9707	3	9.573	82.648	10	2.0	26.5	7.0	148	2.0	9	61	15.50	2.00	2.80	8.00	5.10	6.00

Table 1 continued

Lake name	Lake code	Sample code	Eco reg	Lat (°N)	Lon (°W)	Ele (m)	Depth (m)	MAT (°C)	pH	Conduct (µS cm <sup>-1</sup> )	O <sub>2</sub> (mg l <sup>-1</sup> )	CO <sub>2</sub> (mg l <sup>-1</sup> )	Alk (mg l <sup>-1</sup> )	Ca <sup>2+</sup> (mg l <sup>-1</sup> )	Mg <sup>2+</sup> (mg l <sup>-1</sup> )	K <sup>+</sup> (mg l <sup>-1</sup> )	Na <sup>+</sup> (mg l <sup>-1</sup> )	Si (mg l <sup>-1</sup> )	Cl <sup>-</sup> (mg l <sup>-1</sup> )
Morrenas	60	0301	7	9.492	83.485	3,496	3.0	7.7			4.9			2.28	1.98	0.13	1.38	1.74	0.06
Morrenas	61	9802	7	9.495	83.490	3,475	1.3	7.8			4.9			3.79	0.50	0.14	1.55	2.96	0.07
Morrenas	62	9802	7	9.498	83.490	3,472	8.1	7.8			5.2			4.11	0.40	0.06	1.14	2.57	0.03
Morrenas	63	9802	7	9.500	83.489	3,466	3.0	7.8			5.2			4.86	0.59	0.08	1.45	2.92	0.01
Ditkebi	65	0301	7	9.470	83.482	3,493	7.0	7.7						4.59	1.33	0.06	1.11	2.27	0.08
Cuipiapa	66	9803	1	10.670	85.164	480	2.0	24.0	7.1	94	7.0	7	47	12.08	5.38	2.15	7.34	23.81	5.10
Estero Blanco	67	9803	1	10.668	85.201	430	3.2	24.3	7.9	214	7.6	6	75	18.10	6.39	4.63	11.69	15.07	4.47
Los Juncos Far	68	9803	1	10.669	85.190	440	1.8	24.2	6.8	136	9.3	7	78	6.19	3.33	7.04	7.67	12.26	4.92
Los Juncos Near	69	9803	1	10.668	85.191	440	3.0	24.2	7.5	119	10.7	4	56	9.25	3.36	8.46	7.62	11.11	5.94
San Pablo	71	9803	1	10.662	85.179	450	2.5	24.2	9.5	176	12.0	7	95	17.72	2.37	6.46	15.71	28.33	7.24
Espabelosa	72	9803	1	10.660	85.183	440	3.0	24.2						4.71	1.68	4.91	12.98	42.41	5.47
Ramírez	73	9803	5	10.732	85.017	570	2.5	23.5						4.71	1.68	2.45	3.36	8.70	3.16
Copey	74	9903	5	10.139	84.093	2,460	2.0	13.3						0.20	0.20	1.10	0.30	0.70	8.70
Chirripó 2	79	0003	7	9.483	83.501	3,495	4.0	7.7						3.87	0.19	0.00	0.90	0.65	0.10
Chirripó 3	80	0003	7	9.484	83.504	3,457	4.0	7.9						5.69	0.42	0.00	2.66	1.55	0.10
Morrenas	81	0103	7	9.497	83.491	3,494	0.3	7.7						2.08	0.20	0.14	1.15	1.85	0.18
Sorpresa	87	0103	1	10.711	85.211	570	0.8	23.5	6.7	145	0.6	23	60	8.91	2.70	4.11	12.21	3.96	5.40
Martínez	88	0103	2	10.642	85.197	330	3.6	24.8	6.4	45				28.02	8.87	5.70	24.54	33.32	4.81

Lake code corresponds to lake numbering system in previous limnological studies (Horn & Haberyan, 1993, in press; Haberyan et al., 2003). Sample code represents the time when the sediment samples were collected (e.g., "9107" = 1991 July). Lakes with a full suite of limnological and climate data used in CCA are highlighted in bold ( $n = 39$ )

Lat latitude, Lon longitude, Ele elevation (m a.s.l.), MAT mean annual air temperature, Eco reg ecosystem region, after Kappelle (2014/2015), and the region codes are: 1 northern Pacific lowland deciduous dry forest, 2 Nicoya-Tempisque Pacific dry forest, 3 Caribbean lowland evergreen moist forest, 4 southern Pacific lowland evergreen moist forest, 5 northern highland evergreen moist forest, 6 southern highland evergreen cloud forest, 7 southern highland páramo grassland

et al. (2008), and Cranston (2010) providing additional diagnostic information.

### Statistical analyses

A form of indirect gradient analysis, detrended correspondence analysis (DCA), was used to identify patterns in the variation in the distribution of chironomids and identify the length of the environmental gradients captured by the training set to establish whether the constrained ordinations should be based on an underlying linear or unimodal response model (ter Braak & Prentice, 1988; Pienitz et al., 1995; ter Braak & Verdonschot, 1995). The form of direct gradient analysis that is most appropriate to assess relationships between chironomid distribution and environmental variables when lengthy environmental gradients have been sampled, e.g.,  $>4$  SDs, is canonical correspondence analysis (CCA) (ter Braak & Verdonschot, 1995; Birks, 1995).

The length of DCA axis 1 indicated that the correspondence between chironomid distribution and the measured limnological variables could be evaluated using CCA. A series of CCAs, constrained to individual environmental variables, were implemented to determine a subset of the variables that could explain a statistically significant amount of variation ( $P \leq 0.05$ ) in the chironomid distribution. The statistical significance of each variable was assessed using Monte–Carlo permutation tests (499 permutations). The CCA was based on the covariance matrix of the square-root transformed species data. Of the 14 available environmental variables, 12 were removed from further analyses because they did not account for a statistically significant amount of variance ( $P > 0.05$ ); the variables that were removed were: elevation, depth, pH, O<sub>2</sub>, CO<sub>2</sub>, alkalinity, Ca<sup>2+</sup>, Mg<sup>2+</sup>, K<sup>+</sup>, Na<sup>+</sup>, Si, and Cl<sup>-</sup>. Two environmental variables were identified as accounting for a statistically significant amount of variance in the sub-fossil chironomid distribution. The amount of statistically significant and independent variance captured by these two variables was determined using a series of partial CCAs.

All numeric analyses were undertaken on chironomid taxa that were present in at least two lakes with a relative abundance of 2% in at least one lake; taxa that did not meet this criterion were removed from further analysis. The relative abundance of the chironomid

taxa were square-root transformed to optimize the “signal” to “noise” ratio and stabilize the variance in the chironomid data (Prentice, 1980). In all DCAs and CCAs, rare taxa were down weighted. CANOCO 4.5 (ter Braak & Šmilauer, 2002) was used to implement all ordination analyses. Chironomid-based transfer functions or inference models for temperature (MAT) were created using weighted-averaging (WA), partial least squares (PLS), and weighted-averaging partial least squares (WA–PLS) and implemented using the program C2 (Juggins, 2003). Samples were considered as outliers if their absolute residuals (predicted–observed) were greater than 1 SD of the variable of interest (Jones & Juggins, 1995; Lotter et al., 1997; Porinču & Cwynar, 2000). In this study, 44 lakes of the original 51 lakes were incorporated in the final chironomid-based MAT inference model. The lakes that were removed from the inference model are Tres de Junío, Asunción, Cote, Fraijanes, Sierpe, Vueltas, and San Miguel. The predicative error associated with the inference models was determined using leave-one-out cross-validation, i.e., jack-knifing (Birks, 1998).

### Results

Fifty-six chironomid taxa, including two unknown types, were identified in the 51 surface sediment samples. Of the 56 chironomid taxa, 45 taxa met the initial screening criterion. These 45 taxa accounted for between 89.4 and 100% of the total chironomid remains enumerated per sample. The midge taxa, *Unknown i*, was present only in one lake, Quebrador, with a relative abundance of 10.6%; however, *Unknown i* is regarded as rare taxon following the screening criterion and was removed from statistical analyses. The length of DCA axis 1 and axis 2 was 3.07 and 1.73 SD units, respectively. The eigenvalues of the first two DCA axes were 0.40 and 0.18, indicating these two axes captured 58% of the variance in the chironomid assemblages. The length of the DCA axis 1 suggests that direct gradient analyses can be based on either a unimodal, e.g., CCA or linear, e.g., redundancy analysis (RDA), approach (Lepš & Šmilauer, 2003).

The chironomid percentage diagram, with the taxa grouped into three subfamilies, Chironominae, Orthocladiinae and Tanypodiane, reveals a strong relationship between elevation, and by extension MAT and

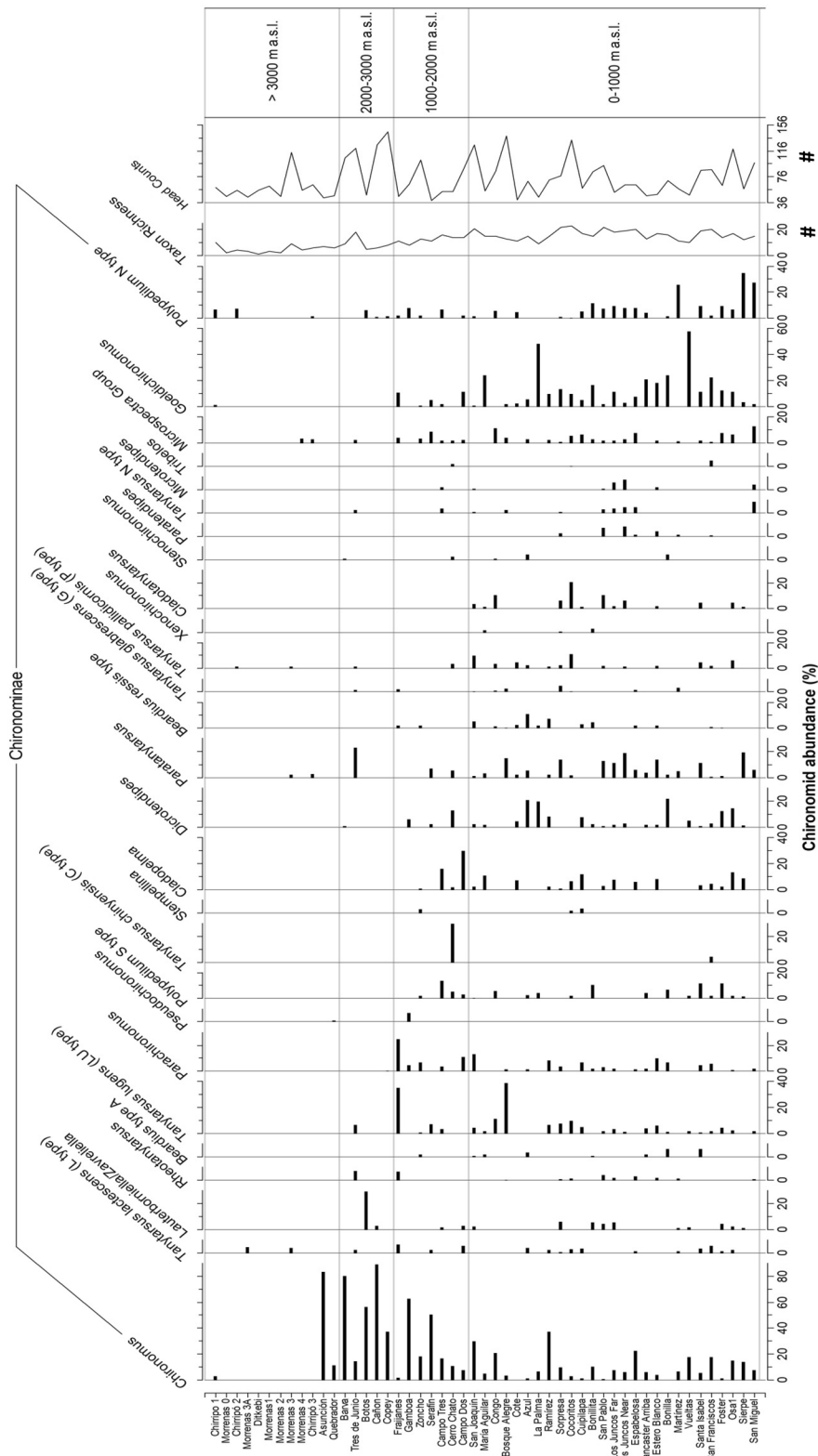
chironomid distribution (Fig. 2). Orthoclaadiinae such as *Psectrocladius*, *Cricotopus*, and *Limnophyes* are most abundant in the high-elevation lakes with low MAT, but are absent in the lower elevation lakes. Chironominae such as *Dicrotendipes*, *Geoldichironomus*, *Cladotanytarsus*, and *Polypedilum N* type are most consistently found in low-elevation lakes with high MAT, and *Chironomus* is commonly observed in mid- to high-elevation lakes with relatively low MAT. Other Chironominae taxa, e.g., *Micropsectra* group and *Tanytarsus L* type, are broadly distributed and appear to be eurythermic. Tanypodinae such as *Procladius* are widely distributed, whereas, *Labrundinia* is restricted to mid- to low-elevations lakes with relatively high MAT. The midge assemblages found in mid-elevation lakes are characterized by a relative high abundance of *Parachironomus*, *Cladopelma*, and *Tanytarsus L* type. *Psectrocladius*, *Chironomus*, and *Procladius* are the most abundant genera in the Orthoclaadiinae, Chironominae, and Tanypodinae sub-families, respectively. The taxon richness across the training set, which ranges from 1 to 23, generally decreases with increased elevation (Fig. 2). The minimum richness is found in Lake Ditkebi, a glacial lake at 3,493 m a.s.l., with only one taxon (*Procladius*) observed. Maximum taxon richness is observed in Cocoritos, a shallow (depth = 1 m), warm (MAT = 23.8°C), mid-elevation (520 m a.s.l) lake with relatively high conductivity (114  $\mu\text{S cm}^{-1}$ ). The total head counts of chironomids are generally the highest in mid-elevation lakes (Fig. 2).

Full limnological data were available for 39 of the 51 lakes in the training set (Table 1). CCA, implemented using the 14 environmental variables as individual predictors, determined that two variables, MAT and conductivity, could account for a statistically significant amount of variance ( $P \leq 0.05$ ) in the distribution of sub-fossil chironomids in the 39-lake dataset (Table 2). The eigenvalues of the first axis and second axis of a CCA constrained to these two variables were 0.27 and 0.05, respectively. These two axes captured 26.9% of the total variance in chironomid communities in the dataset. The species–environment correlations for the first two axes were 86.4 and 76.8%, respectively. Both CCA axes were statistically significant ( $P \leq 0.05$ ) based on Monte–Carlo permutation tests (499 unrestricted permutations). Partial CCAs identified that amount of variance captured solely by MAT and independently of conductivity is 12.3 and 10.1%,

respectively (Table 3). The partial CCAs also determined that the amount of variance captured by MAT independent of lake chemistry is 12.4% ( $P < 0.05$ ) and independent of the other physical variables is 3.0% ( $P > 0.05$ ) (Table 3).

Biplots depicting the results of the CCA of the chironomid taxa present in the 39-lake training set and MAT and conductivity are depicted in Fig. 3a and b. The length of the arrow representing the environmental variables is proportional to the relative importance of the variable and the angle of the arrow describes the relationship of the variable to each of the CCA axes (ter Braak & Prentice, 1988; ter Braak & Verdonschot, 1995). MAT is strongly correlated with CCA axis 1, whereas conductivity is related to CCA axis 2. The CCA identified two distinct groups of lakes (Fig. 3a). The first group, in the right half of the diagram, includes Chirripó 1, Morrenas 1, Asunción, Quebrador, Barva, Tres de Junío, Botos, and Cañon (lake names not labeled). These eight lakes are all located above 2,400 m a.s.l. and their MATs range from 7.5 to 13.2°C with an average MAT of 11.1°C. The lakes associated with the second group are tightly clustered on the left side of the diagram, indicating the existence of less variability in the lowland chironomid communities. Lakes in this group are located between 0 and 1,000 m a.s.l., have an average MAT of 24.3°C, and span a temperature range from 21.3 to 26.5°C. La Palma, a low-elevation lake (570 m a.s.l.) that loads high on CCA axis 1, is a notable outlier relative to the other low-elevation lakes (Fig. 3a). This is likely because Lake La Palma is a deep lake (depth = 10.8 m) with the highest conductivity (293  $\mu\text{S cm}^{-1}$ ) in the training set. Mid-elevation lakes, defined as lakes located between 1,000 and 2,000 m a.s.l., are scattered near the origin. In the CCA biplot of chironomid taxa (Fig. 3b), taxa such as *Psectrocladius*, *Limnophyes*, *Unknown ii*, and *Cricotopus* are most abundant in lakes located above 2,000 m a.s.l., and are separated from *Cladopelma*, *Cladotanytarsus*, *Polypedilum N/S* type, *Tribelos*, and *Labrundinia*, which are most abundant in warm lakes with low conductivity. The CCA illustrates that *Pseudochironomus*, *Parametriocnemus*, and *Procladius* (lower right quadrant) are most abundant in lakes with low MAT and conductivity, whereas taxa such as *Microtendipes*, *Dicrotendipes*, *Larsia*, and *Geoldichironomus*, found in the top left quadrant, are associated with lakes with high MAT and





**Fig. 2** Modern distribution of chironomids in the training set of 51 lakes, arranged by elevation. All the chironomids are present in two or more lakes with abundance  $\geq 2\%$  at least in one lake

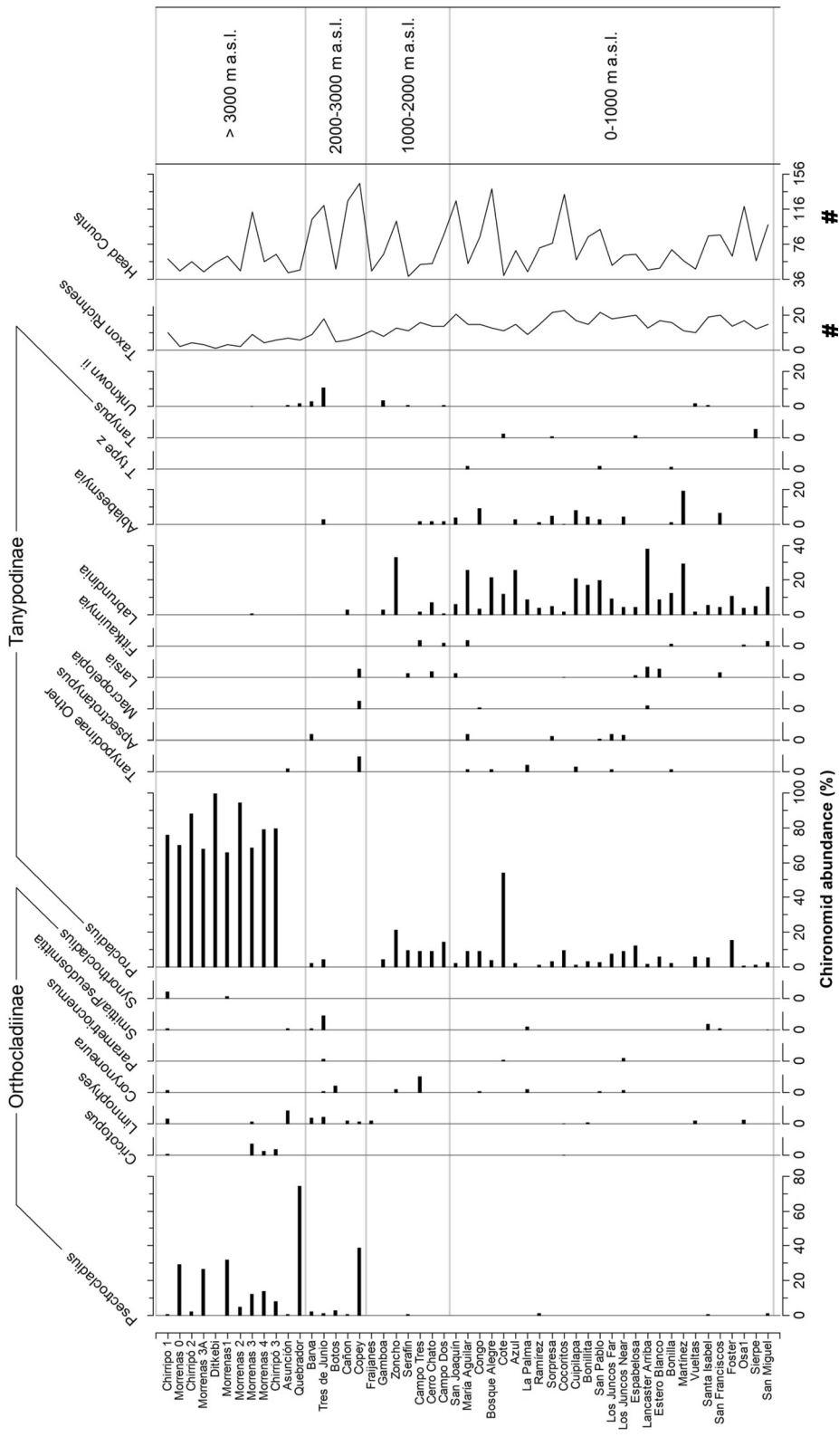


Fig. 2 continued

conductivity. Taxa such as *Stenochironomus*, *Apsectrotanypus*, and *Rheotanytarsus*, which load high on CCA axis 2, are associated with moderate MAT and high conductivity. *Xenochironomus*, *Tanypus*, and *Fittkauimyia* load highly on the negative end of CCA axis 2, reflecting that these taxa are most abundant in relatively warm lakes with dilute water.

Inference models for MAT were developed using WA, PLS, and WA-PLS (Table 4). Based on a high coefficient of determination ( $r_{\text{jack}}^2$ ), low RMSEP, and relatively low maximum bias, a two-component PLS inference model was identified as the best model for MAT. The performance statistics for the MAT inference model are robust with an  $r_{\text{jack}}^2 = 0.94$ , RMSEP = 1.73°C, and the maximum bias = 2.07°C. Graphs of the estimated versus predicted MAT and associated residuals are plotted in Figs. 4 and 5. No obvious trend is apparent in the distribution of the residuals (Fig. 5). The temperature optima and tolerances of the 33 taxa with a Hill's N2 value >5 are plotted in Fig. 6. Taxa with Hill's N2 value >5 in a calibration set could be considered well represented and can provide reliable estimates of temperature optima (Brooks & Birks, 2001).

## Discussion

Numerous studies have been undertaken during recent decades assessing the relationship between the modern

**Table 2** The ratios of the eigenvalue ( $\lambda$ ) of the first (constrained) CCA axis to the eigenvalue of the second (unconstrained) CCA axis based on the 39-lake calibration set sub-set

Environmental variable	$\lambda_1$	$\lambda_2$	$\lambda_1/\lambda_2$	% Variance	P value
MAT	0.268	0.243	1.10	12.3	0.002
Conductivity	0.109	0.347	0.31	5.0	0.022

**Table 3** Summary of partial CCAs based on chironomid assemblages from the 39-lake subset of the training set

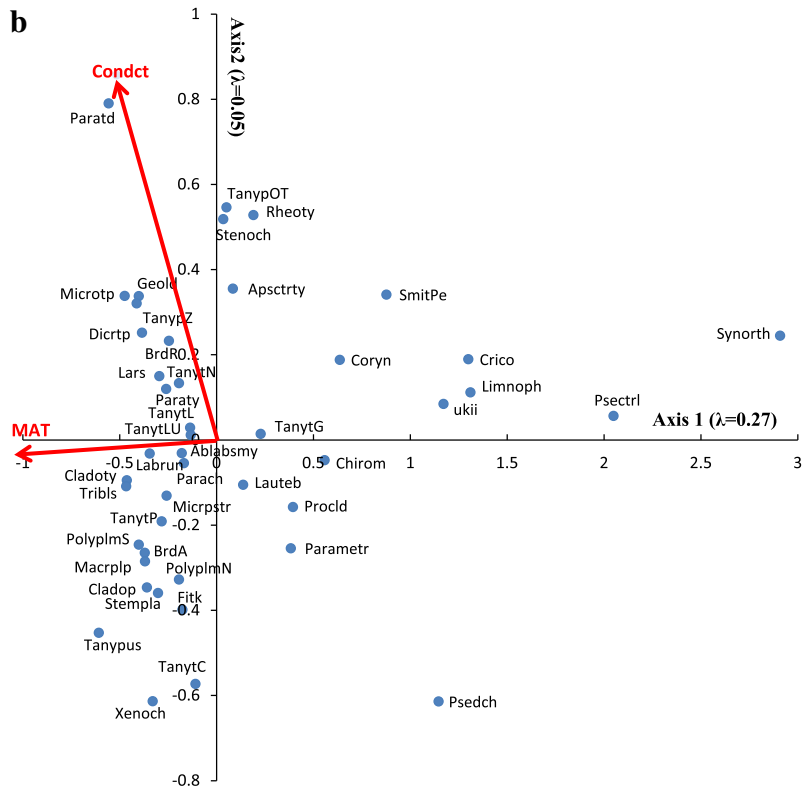
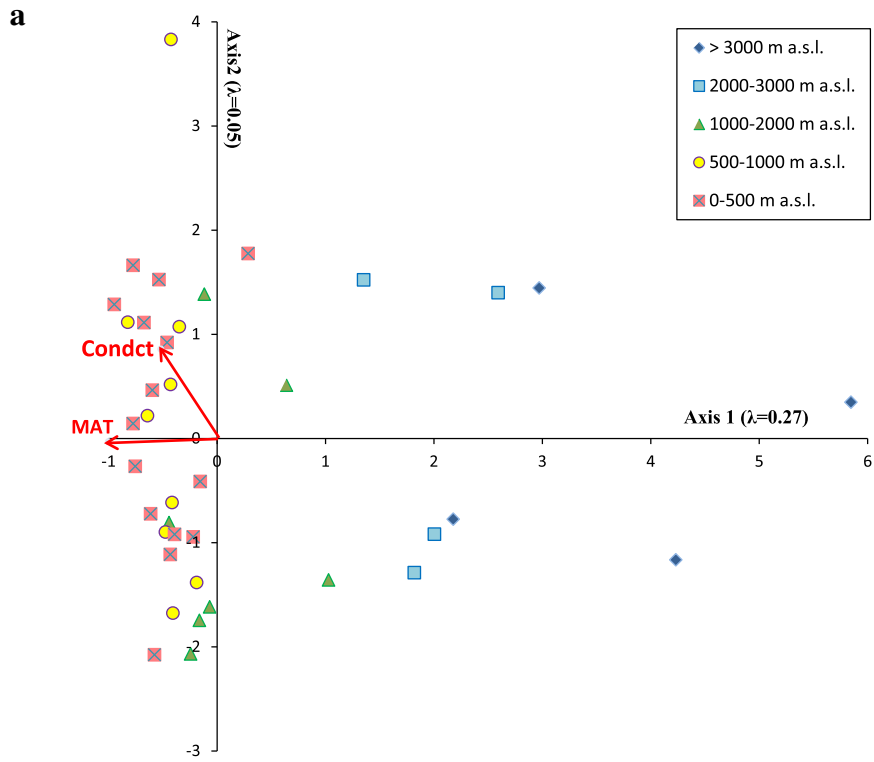
Environmental variable	Covariate(s)	$\lambda_1$	$\lambda_2$	$\lambda_1/\lambda_2$	% Variance	P value
MAT	None	0.268	0.243	1.10	12.3	0.002
	Conductivity	0.210	0.243	0.86	10.1	0.002
	Lake Chemistry	0.197	0.213	0.92	12.4	0.002
	Lake physical	0.055	0.241	0.23	3.0	0.386

Lake chemistry = pH, conductivity, O<sub>2</sub>, CO<sub>2</sub>, Alk, Ca<sup>2+</sup>, Mg<sup>2+</sup>, K<sup>+</sup>, Na<sup>+</sup>, Si, Cl<sup>-</sup>; Lake physical = depth and elevation

distribution of sub-fossil chironomids and physical and chemical conditions in freshwater ecosystems (Walker & Mathewes, 1989; Walker et al., 1991a, 1997; Wilson et al., 1993; Olander et al., 1997, 1999; Lotter et al., 1997; Porinchu & Cwynar, 2000; Porinchu et al., 2009; Porinchu et al. 2010; Nazarova et al., 2011, Self et al., 2011; Haskett & Porinchu, in press). This is the first study that has assessed the contemporaneous relationship between the distribution of sub-fossil chironomids and limnological and climatic parameters in Central America.

A number of chironomid faunal surveys have been conducted in recent decades in Central America with a limited number undertaken in Costa Rica (Watson & Heyn, 1992; Spies & Reiss, 1996; Spies et al., 2009; Kranzfelder, 2012). Watson & Heyn (1992) collected Chironomidae from 40 localities in Costa Rica, most of which were lotic habitats, across a broad elevational gradient. They identified 55 chironomid genera, including approximately 148 species. Chironominae and Orthoclaadiinae dominated the assemblages, with *Cricotopus* the most abundant and diverse genus (Watson & Heyn, 1992). A comprehensive inventory of neotropical and Mexican Chironomidae by Spies & Reiss (1996) cataloged 709 species. More recent work provides detailed descriptions of neotropical and Costa Rican chironomid taxonomy; however, the taxonomic identifications were based on the imago or adult stage of the insect (Spies & Reiss, 1996; Spies et al., 2009; Kranzfelder 2012). Neither survey provided photomicrographs illustrating diagnostic features of chironomid taxa and therefore did not provide guidance for the taxonomic identification of the sub-fossil chironomid head capsules encountered in this study.

The CCA site-biplot indicates that lakes in the training set can be classified into two distinct groups (Fig. 3a). One group includes most of the low-elevation



◀ **Fig. 3** **a** CCA bi-plots illustrating the relationship between the 39-lake training set sub-set classified by elevation and the two forward selected environmental variables (MAT and conductivity). Lakes are color-coded according to elevation. *MAT* mean annual air temperature, *Conduct* conductivity. **b** CCA correlation bi-plot illustrating the relationship between the 45 chironomid taxa in the 39-lake training set sub-set and the two forward selected variables (MAT and conductivity). Abbreviations for chironomid taxa: Ablabsm = *Ablabesmyia*; Apsctrry = *Apsectrotanypus*; BrdA = *Beardius A* type; BrdR = *Beardius reissi* type; Chironom = *Chironomus*; Cladop = *Cladopelma*; Coryn = *Corynoneura C/E* type; Crico = *Cricotopus*; Dictrp = *Dicrotendipes*; Fitk = *Fittkauimyia*; Goeld = *Goeldichironomus*; Labrun = *Labrundinia*; Lars = *Larsia*; Lauteb = *Lauterborniella/Zavreliella*; Limnoph = *Limnophyes*; Macrpplp = *Macropelopia*; Microtp = *Microtendipes*; Micrpstr = *Micropsectra*; Parach = *Parachironomus*; Parametr = *Parametriocnemus*; Paratd = *Paratendipes*; Paraty = *Paratanytarsus*; PolyplmN = *Polypedilum N* type; PolyplmS = *Polypedilum S* type; Procl = *Procladius*; Psectrcl = *Psectrocladius*; Pseudch = *Pseudochironomus*; Rheoty = *Rheotanytarsus*; SmitPe = *Smittia/Pseudosmittia*; Stenoch = *Stenochironomus*; Synorth = *Synorthocladius*; TanypOT = Tanypodinae other; Tanyps = *Tanypus*; Tanypz = *Tanypodinae Z* type; TanytC = *Tanytarsus C* type; TanytG = *Tanytarsus G* type; TanytL = *Tanytarsus L* type; TanytLu = *Tanytarsus LU* type; TanytN = *Tanytarsus N* type; TanytP = *Tanytarsus P* type; Tribels = *Tribelos*; Ukii = *Unknown ii*; Xenoch = *Xenochironomus*

lakes (0–1,000 m a.s.l.) with relatively high MAT. For example, the measured MAT of Lake Cote (650 m a.s.l.), Lake Estero Blanco (430 m a.s.l.), and Lake Sierpe (16 m a.s.l.) are 23.1, 24.3, and 26.5°C, respectively. The average MAT for the low-elevation lakes ( $n = 27$ ) is 24.3°C. Lake La Palma, a 10.8 m deep lake with a maximum conductivity of 293  $\mu\text{S cm}^{-1}$  m loads highly on CCA axis 1. This high loading results from the extremely high relative abundance of *Geoldichironomus* type (48.3%) and *Dicrotendipes* (20.2%) and likely reflects the influence of thermal stratification and water chemistry on the La Palma chironomid community. The second group consists of high-elevation lakes

(2,000–3,500 m a.s.l.) with low MATs. The average MAT for this group ( $n = 17$ ) is 8.0°C.

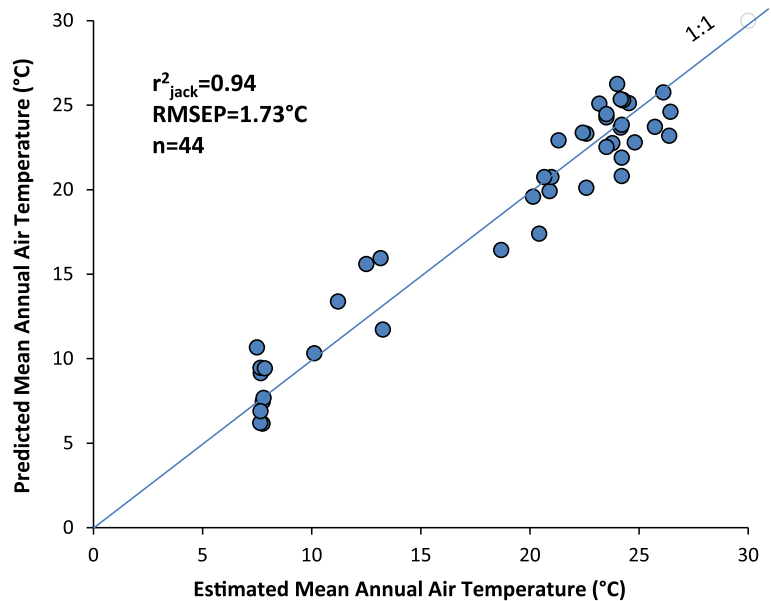
The CCA-biplot diagram of species scores (Fig. 3b) reveals that *Microtendipes*, *Geoldichironomus*, *Dicrotendipes*, *Larsia*, *Beardius reissi* type, and *Paratanytarsus* are associated with high MAT and conductivity. The distribution of these chironomids in Costa Rica is consistent with previous work that has identified *Microtendipes* and *Dicrotendipes* as thermophilous taxa (Brooks & Birks, 2001; Brooks et al., 2007). In this study, *Microtendipes*, *Geoldichironomus*, *Dicrotendipes*, *Paratanytarsus*, *Beardius reissi* type, and *Larsia* are most abundant in warm lakes with an average MAT of 23.2 ( $\pm 2.8$ )°C. *Psectrocladius* is ubiquitous and abundant, occurring in 20 of the training set lakes. *Psectrocladius* dominates the chironomid assemblage in Lake Quebrador and Lake Copey, with a relative abundance of 74.5 and 39.0%, respectively. These two lakes are characterized by low MAT (10.1–13.3°C) and ion concentration. Walker & Mathewes (1989) identified *Psectrocladius* as a common constituent of low-elevation lakes in British Columbia and Brundin (1949) identified *Psectrocladius* as an important constituent of temperate lakes in North America. Our results indicate that *Psectrocladius* appears to have a more restricted range in Costa Rica, relative to previous studies. It is largely restricted to high-elevation lakes with low MAT in Costa Rica. *Limnophyes*, a semi-terrestrial taxon (Armitage et al., 1995), is most abundant in high-elevation lakes with low MAT (Fig. 3b). *Rheotanytarsus*, which is found in 11 lakes, has a relatively high abundance (7.5%) in Tres de Junio along with *Unknown ii* type (11.25%) (Fig. 2). Tres de Junio is a small pond in an area of poorly drained land surrounded by bog vegetation and characterized by high levels of organic matter (Horn & Haberyan, 1993). *Geoldichironomus*, a widely distributed taxon

**Table 4** Performance statistics for the six different chironomid-based inference models developed for mean annual air temperature (MAT)

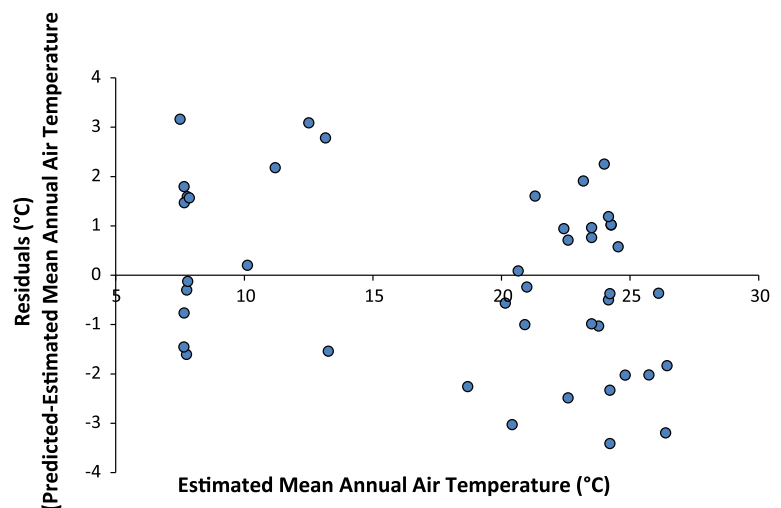
Inference model	Apparent		Cross-validation		Maximum bias (°C)
	RMSE (°C)	$r^2$	RMSEP (°C)	$r^2$	
WA (inverse)	2.61	0.86	3.11	0.80	5.10
WA (classical)	2.81	0.86	3.29	0.80	4.94
WA-PLS (3-component)	1.34	0.96	2.02	0.92	1.97
PLS (1-component)	2.01	0.92	5.66	0.89	2.29
<b>PLS (2-component)</b>	<b>1.44</b>	<b>0.96</b>	<b>1.73</b>	<b>0.94</b>	<b>2.07</b>

The best model is bolded

**Fig. 4** Relationship between estimated and chironomid-inferred (jack-knifed) mean annual air temperature (MAT) based on a two-component PLS model. Estimated MAT is derived from application of the lapse rate reported in Orvis & Horn (2000)



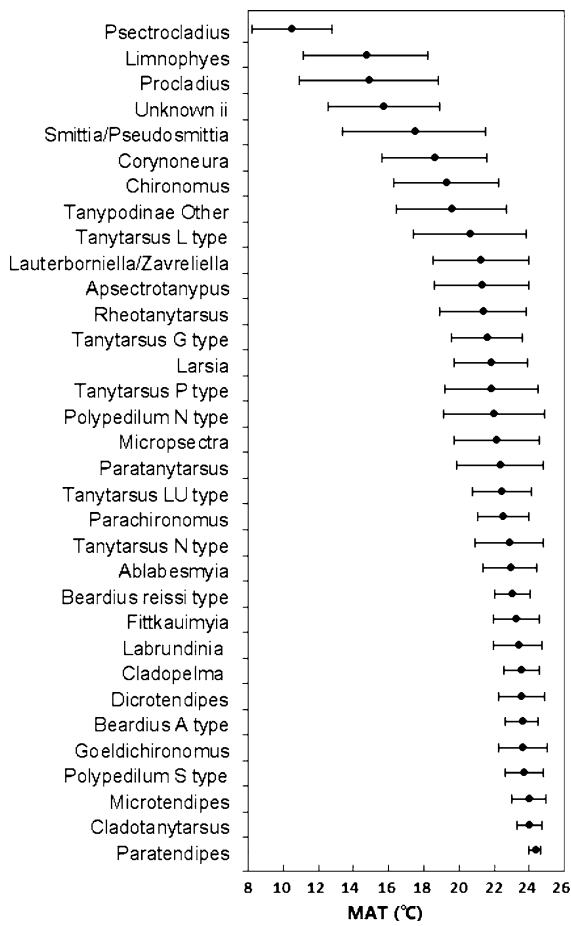
**Fig. 5** Residuals (predicted–estimated) for MAT based on a two-component PLS model. Estimated MAT is derived from application of the lapse rate reported in Orvis & Horn (2000)



in the Costa Rican training set, is very abundant (>50%) in two lakes, La Palma and Vueltas (Fig. 2). These lakes are characterized by high MAT (23.5–25.1°C), conductivity (233–293  $\mu\text{S cm}^{-1}$ ), and pH (8.2–8.7).

This is the first report of *Psectrocladius* in Costa Rica. Two additional taxa encountered in this study—*Unknown i* and *Unknown ii*—do not appear to be recorded in existing checklists of Central American Chironomidae (Watson & Heyn, 1992; Spies & Reiss, 1996; Spies et al., 2009; Kranzfelder, 2012). *Unknown i* (Fig. 7B) is only found in Quebrador, a shallow,

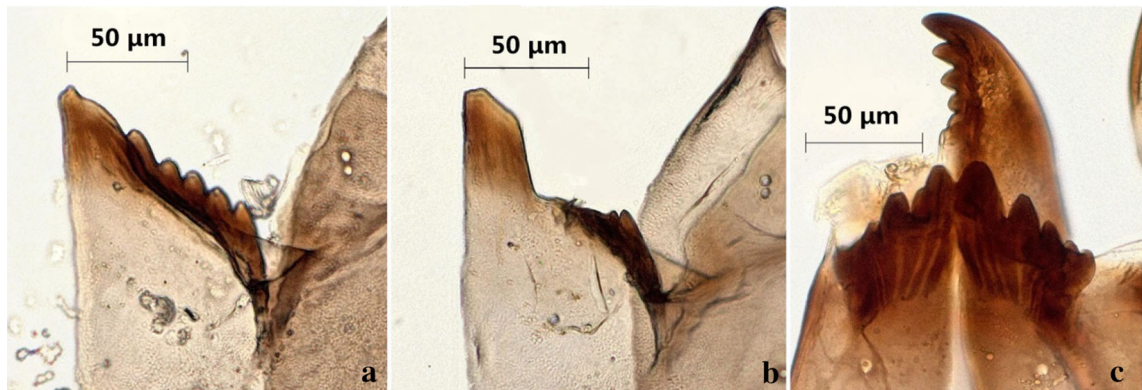
dilute (conductivity = 0  $\mu\text{S cm}^{-1}$ ), high-elevation lake, located at 3,040 m a.s.l., and characterized by low taxa richness ( $n = 5$ ). *Psectrocladius* and *Unknown ii* (Fig. 7A, C) are restricted to lakes with relatively low MAT (Figs. 2 and 3b). The MAT optima for *Psectrocladius* and *Unknown ii* are  $10.4 \pm 2.4^\circ\text{C}$  and  $15.7 \pm 3.2^\circ\text{C}$ , respectively (Fig. 6). Interestingly, *Psectrocladius* is abundant in the glacial lakes surrounding Cerro Chirripó: Chirripó 1, 2 and 3 and Morrenas 0, 1, 2, 3, 3a and 4. The maximum abundance of *Psectrocladius* (74.5%) is found in Quebrador, an artificial lake at high elevation



**Fig. 6** Weighted-average MAT optima (solid circle) and tolerance (thick lines with ticks) of the 33 chironomid taxa with Hill’s N2 values >5 in the training set

that shares characteristics as the glacial lakes—low MAT and extremely low conductivity. The distribution and abundance of *Psectrocladius*, *Unknown i*, and *Unknown ii* in our study may reveal that these taxa are absent from the existing checklists due to the limited number of collections undertaken at high elevations (Watson & Heyn, 1992; Spies & Reiss, 1996).

The influence of air and water temperature on chironomids has been recognized for some time (Brundin, 1949, 1956). Developmental rates, emergence, and voltinism of chironomid larvae are influenced by air temperature (Brundin, 1949; Ward & Cummins, 1978; Menzie, 1981; Walker & Mathewes, 1989). Strong correlations between air temperature and modern chironomid communities have been found in a number of arctic, temperate, and tropical areas (Eggermont et al., 2010). In our study, CCA indicated that MAT and conductivity are significantly correlated with the distribution of chironomids in Costa Rica. Of these two variables, MAT explained the greatest amount of variance in the chironomid communities, agreeing with results from calibration sets developed in arctic, sub-arctic, and alpine environments (Brooks, 2006; Walker & Cwynar, 2006; Eggermont et al., 2010). These previous studies have all shown that MAT can account for an independent and statistically significant amount of variance in the distribution of chironomids across broad geographic regions. Recent research has also identified the existence of a strong, statistically significant relationship between chironomids and temperature



**Fig. 7** Photomicrographs of three chironomid taxa reported for the first time from Costa Rica. **A** *Psectrocladius*, **B** *unknown i*, and **C** *unknown ii*

in the tropics, although the development and application of chironomid-based temperature inference models in tropical regions is limited. Eggermont et al. (2010) described the modern distribution of African chironomid communities by surveying subfossil chironomid assemblages in the surface sediments of 65 lakes and permanent pools across a ~4,000 m elevation range in southwestern Uganda and central and southern Kenya. Eggermont et al. (2010) assessed the feasibility of using subfossil chironomid communities to develop paleotemperature reconstructions in the African tropics and demonstrated that surface water temperature (SWTemp) and mean annual air temperature (MATemp) for their study sites had a high coefficient of determination ( $r_{\text{jack}}^2 = 0.97$  for MATemp and  $r_{\text{jack}}^2 = 0.95$  for SWTemp) and low root-mean-squared error of prediction ( $\text{RMSEP}_{\text{SWTemp}} = 2.0^\circ\text{C}$ ,  $\text{RMSEP}_{\text{MATemp}} = 1.6^\circ\text{C}$ ). Mean annual air temperature (MATemp) was inferred by different transfer functions; weighted-average based MATemp optima for East African Chironomidae ranged from 1.5 to 23.8°C. Taxa with low MATemp optima (~17.0–25.0°C) had a broader tolerance ( $\pm 4$ –6.0°C) than taxa with relatively high SWTemp optima (~25.0–28.0°C) (Eggermont et al., 2010).

The temperature optima and tolerances for 33 out of 45 taxa encountered in our study are plotted in Fig. 6. Taxa with low MAT optima (10.4–22.3°C) have a broader tolerance (~ $\pm 2.0$ –4.1°C) than taxa with relatively high MAT optima (22.4–24.3°C) with an average MAT tolerance of  $\pm 1.2^\circ\text{C}$ . *Psectrocladius*, which dominated the chironomid communities found in the high-elevation lakes, is characterized by the lowest MAT optimum (10.4°C). This finding does not correspond to the results found in the previous studies, which indicate that *Psectrocladius* is usually associated with temperate lakes (Porinchi & MacDonald, 2003; Brooks et al., 2007; Porinchi et al., 2007) and is even considered as a thermophilous taxon (Brooks et al., 2007; Porinchi et al., 2009).

An important but unresolved question is whether a relationship exists between the distribution of chironomids in Costa Rica and lake productivity and nutrient status. Chironomids have long been used as bioindicators of lake trophic status (Thienemann, 1921). In many chironomid training sets, nutrient availability and other measures of lake productivity or trophic status account for large, statistically significant amounts of variance in chironomid distributions

(Johnson & McNeil, 1988; Brodersen & Lindegaard, 1999; Brodersen & Anderson, 2002; Massaferrero & Brooks, 2002; Brodersen & Quinlan, 2006; Luoto, 2011; Verbruggen et al., 2011). Nutrient status and quantitative estimates of lake productivity are not available for the training set lakes. As a result, it is not possible to assess the degree to which nutrient availability may have influenced chironomid distribution in the Costa Rican training set. The diversity of processes responsible for lake ontogeny in Costa Rica also complicates the interpretation of chironomid–environment relations. The existing Costa Rica calibration dataset includes oxbow lakes, wetland lakes, artificial lakes (reservoirs), lava- and lahar-dammed lakes, landslide lakes, crater lakes, and glacial lakes. The physical and chemical limnology of these lakes varies greatly due to their mode of formation and their geographical location (Horn & Haberyan, 1993; Haberyan et al., 2003). For instance, La Palma and Cocoritos are located at 570 and 520 m a.s.l., respectively, but the ontogeny of each lake is different: La Palma was formed by volcanism and Cocoritos is a reservoir (Haberyan et al., 2003). The physical and chemical limnology of each lake is distinct. Cocoritos is a shallow (1 m), warm (MAT = 23.8°C), moderately dilute lake (conductivity = 114  $\mu\text{S cm}^{-1}$ ) relative to La Palma (10.8 m, 25.7°C, 293  $\mu\text{S cm}^{-1}$ ) (Table 1). However, while complicating some aspects of the present study, the existence of such a diversity of lake-forming processes in Costa Rica provides an outstanding opportunity in future research to assess the influences of varied geographical and limnological parameters on chironomid community composition.

In this study, 44 lakes of the original 51 lakes were incorporated in the final chironomid-based MAT inference model. Tres de Junío, Asunción, Cote, Fraijanes, Sierpe, Vueltas, and San Miguel were removed from the final MAT inference model due to their absolute residuals being >2 SD of the observed MAT (Birks, 1995, 1998). Asunción (3,340 m a.s.l., pH 4.9) and Tres de Junío (2,670 m a.s.l., pH 5.2) are both high-elevation lakes characterized by remarkably low pH values and conductivity but the highest abundance of *Chironomus* (83.7%) and *Partantarsus* (23.3%), respectively. *Chironomus* is broadly distributed in 40 lakes mainly located between 1,000 and 2,000 m a.s.l. Asunción is the only lake located above 3,000 m a.s.l. with a high percentage of *Chironomus*. *Paratantarsus* is found in 25 lakes in the training set



with average abundance of 7.3%. Three of the four lakes with relatively high abundance (15–19%) of this taxon are located at <1,000 m a.s.l.; the fourth lake is Tres de Junio at high elevation. The poor fit of chironomid-inferred temperature at Asunción and Tres de Junio is likely related to the low pH value of these water bodies and the high abundance of these two taxa. Cote is a deep crater lake (depth = 11 m) that is also dominated by a single chironomid taxon, *Procladius* (54.3%), and characterized by very low ion concentrations. Cote is the only low-elevation lake (650 m a.s.l.) out of the 11 lakes that have >50% *Procladius*; the other 10 lakes are all found above 3,000 m a.s.l. Lake depth is likely influencing the chironomid assemblage at Cote and confounding the chironomid–temperature relationship. Fraijanes (1,650 m a.s.l.) is a 6.2-m deep lake characterized by moderately high conductivity (90  $\mu\text{S cm}^{-1}$ ) and the high abundance of *Tanytarsus lugens* type (35.2%). In the training set, *Tanytarsus lugens* type is mainly found below 1,000 m a.s.l., with the highest abundance of *T. lugens* type occurring at Bosque Alegre (740 m a.s.l.). Bosque Alegre and Fraijanes are separated by approximately 1,000 m in elevation. It is difficult, with the limnological data currently available, to isolate why applying the inference model to the midge assemblage from Fraijanes results in a large residual. The high residuals for Sierpe, San Miguel, and Vueltas, all low-elevation lakes (below 300 m a.s.l.), may be due to the influence that extremely high conductivity may have on midge community composition.

The chironomid-based inference model developed in this study captures the largest altitudinal range (3,510 m a.s.l.) and the second largest air temperature range (19.0°C) of existing chironomid-based air temperature inference models. The RMSEP and  $r_{\text{jack}}^2$  of this inference model is 1.73°C and 0.94, respectively. The MAT range captured in the Costa Rica training set is 19.0°C, resulting in the RMSEP being relatively small when reported as a percentage of the MAT range (9.11%). The two studies conducted in the tropics (Eggermont et al., 2010; this study) used MAT as the inference model parameter due to the existence of low seasonality in the equatorial zone. Although the RMSEP of the inference model developed in this study has an error that is likely similar in magnitude to the expected thermal variability that characterized this

region during the late Holocene, it is important to note that there are no terrestrial-based quantitative records of late Holocene temperature currently available for southern Central America. Application of this model, incorporating consensus approaches and analog tests, to multiple sub-fossil chironomid stratigraphies will facilitate the development of much-needed quantitative temperature reconstructions. These reconstructions can be compared to existing multi-proxy paleoecological studies to provide insight into centennial and millennial-scale temperature trends in this region during the Holocene.

## Conclusions

This is the first attempt at quantifying the modern relationship between chironomid distribution and limnological and climatic parameters in Costa Rica. Direct gradient analyses, i.e., CCA, indicated that MAT, and conductivity are strongly related to the distribution of chironomids in Costa Rica. Of these two variables, MAT explained the greatest variance in the chironomid communities. Inference models for MAT were developed based on chironomid abundance data from 51 lakes. The best model, with a high coefficient of determination ( $r_{\text{jack}}^2 = 0.94$ ), low RMSEP (1.73°C), and low maximum bias (2.02°C), was based on a two-component PLS. The robust performance statistics of the midge-based inference model provides the opportunity to reconstruct Holocene thermal regimes in Costa Rica and potentially elsewhere in Central America. Ongoing research, focused on the application of the quantitative chironomid-based inference model developed in this article to subfossil chironomid assemblages extracted from Laguna Zoncho in southern Costa Rica, will provide quantitative estimates of past temperature change for this region spanning 3,000 years.

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