Bioindicators of climate and trophic state in lowland and highland aquatic ecosystems of the Northern Neotropics

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Abstract: Chironomids, diatoms and microcrustaceans that inhabit aquatic ecosystems of the Northern Neotropics are abundant and diverse. Some species are highly sensitive to changes in water chemical composition and trophic state. This study was undertaken as a first step in developing transfer functions to infer past environmental conditions in the Northern lowland Neotropics. Bioindicator species abundances were related to multiple environmental variables to exploit their use as environmental and paleoenvironmental indicators. We collected and analyzed water and surface sediment samples from 63 waterbodies located along a broad trophic state gradient and steep gradients of altitude (~0-1 560m.a.s.l.) and precipitation (~400-3 200mm/y), from NW Yucatán Peninsula (Mexico) to southern Guatemala. We related 14 limnological variables to relative abundances of 282 diatom species, 66 chironomid morphospecies, 51 species of cladocerans, 29 non-marine ostracode species and six freshwater calanoid copepods. Multivariate statistics indicated that bicarbonate is the strongest driver of chironomid and copepod distribution. Trophic state is the second most important factor that determines chironomid distribution. Conductivity, which is related to the precipitation gradient and marine influence on the Yucatán Peninsula, is the main variable that shapes diatom, ostracode and cladoceran communities. Diatoms, chironomids and cladocerans displayed higher diversities (H=2.4-2.6) than ostracodes and copepods (H=0.7-1.8). Species richness and diversity were greater at lower elevations (<450m.a.s.l.) than at higher elevations in Guatemala. Distribution and diversity of bioindicators are influenced by multiple factors including altitude, precipitation, water chemistry, trophic state and human impact. Rev. Biol. Trop. 61 (2): 603-644. Epub 2013 June 01.

Key words: microcrustaceans, chironomid, diatom, aquatic ecosystems, bioindicators, Northern Neotropics, autecology, diversity.

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Natural and anthropogenic factors influence physical and chemical lake variables and aquatic biota, especially environmentally sensitive phytoplankton, phytobenthos, zooplankton and zoobenthos communities. Such factors include water extraction, pollution, eutrophication, flow modification, changes in water level, habitat degradation, climate warming, and changes in evaporation and precipitation (Dudgeon *et al.* 2006). Continental waterbodies are some of the most endangered ecosystems in the world (Sala *et al.* 2000), especially those in developing countries (Pérez *et al.* 2011a). Waterbodies in the Northern Neotropics are important resources for local inhabitants. They provide drinking water, sites for recreation, navigation, and habitat for both aquatic and terrestrial fauna and flora (Dudgeon *et al.* 2006). Despite their importance, there have been few limnological or ecological studies of these ecosystems, especially in Guatemala and Belize (Pérez *et al.* 2011a). Many local inhabitants around the largest lakes in Guatemala, Lakes Izabal, Petén Itzá, Amatitlán and Atitlán, rely on local fisheries for subsistence and to generate income in local markets. Such activities have affected the trophic state of these lakes. Lake Petén Itzá, located in the Maya Biosphere Reserve in Northern Guatemala still displays high diversity of aquatic bioindicators, but cultural eutrophication in the lake has increased during the last few decades (Rosenmeier *et al.* 2004, Pérez *et al.* 2010a), putting many species at risk. Lake Amatitlán is highly productive and has suffered from cultural eutrophication for decades (Pérez *et al.* 2011a). Aquatic bioindicator diversities in the lake are probably low because of the hypereutrophic conditions. Cyanobacteria dominate the phytoplankton community in the lake, and high rates of decomposition lead to hypoxic or anoxic conditions in deep waters. Cyanobacteria blooms in the lake produce toxins that can be dangerous to humans if present in high concentrations (Pérez *et al.* 2011a*)*.

Aquatic organisms that are sensitive to changes in water chemical composition, pollution and trophic state, i.e. aquatic bioindicators such as diatoms, chironomids and microcrustaceans, are frequently used to track environmental change. Diatoms are generally a dominant group in the phytoplankton, whereas cladocerans, copepods and ostracodes are typically the main zooplankters in fresh waters (Dole-Olivier *et al.* 2000, Walseng *et al.* 2006). Diatoms are unicellular golden-brown algae (Bacillariophyta) characterized by silica shells (frustules) that are well preserved in lake sediments. Diatoms live in planktonic and benthic habitats (Battarbee *et al.* 2001). Chironomids are non-biting midges (Insecta: Diptera) and are frequently the most abundant group of aquatic insects in fresh waters. Chironomids are true flies, but they spend most of their life cycle (egg, larva, pupa) in aquatic habitats (Armitage *et al.* 1995). They are ubiquitous inhabitants of Neotropical aquatic ecosystems. Nevertheless, there have been few studies in the region concerning their taxonomy and autecology (Pérez *et al.* 2010a). Microcrustaceans such as ostracodes, cladocerans and copepods are important organisms in limnological and paleolimnological studies. Ostracodes are typically <3mm long. The two valves that enclose the body are composed of low-Mg calcite (Meisch 2000). Similar to ostracodes, cladocerans are small (0.2-2.5mm). Limbs and a postabdomen extend from a ventral opening in the carapace, facilitating locomotion and feeding (Dole-Olivier *et al.* 2000). Ostracode valves and cladoceran exoskeletons preserve well in lake sediments. Body parts of freshwater copepods (<2.0mm long), however, are poorly preserved. Nevertheless, sacs with resting eggs of some copepod species are robust and well preserved in late Quaternary lake sediments (Bennike 1998). Microcrustaceans, diatoms and chironomids are the main food sources for many aquatic macroinvertebrates and for vertebrates such as fish. They are key components of the food web in lake ecosystems and therefore of great ecological and economic value (Cohen 2003, O'Sullivan & Reynolds 2004). Impacts on these communities from pollution, changes in lake trophic state or climate, can have dramatic consequences for fish populations (Moss

et al. 2003). Microcrustaceans, diatoms and chironomids are widely distributed, can rapidly colonize new habitats (Cohen 2003, Hausmann & Pienitz 2007) and share characteristics that make them useful as bioindicators and paleo-indicators: (1) their well preserved remains in lake sediments can be identified to genus, and sometimes to species level, (2) they are often abundant, (3) they are highly sensitive to environmental changes, (4) they have short life cycles and communities thus respond quickly to environmental changes.
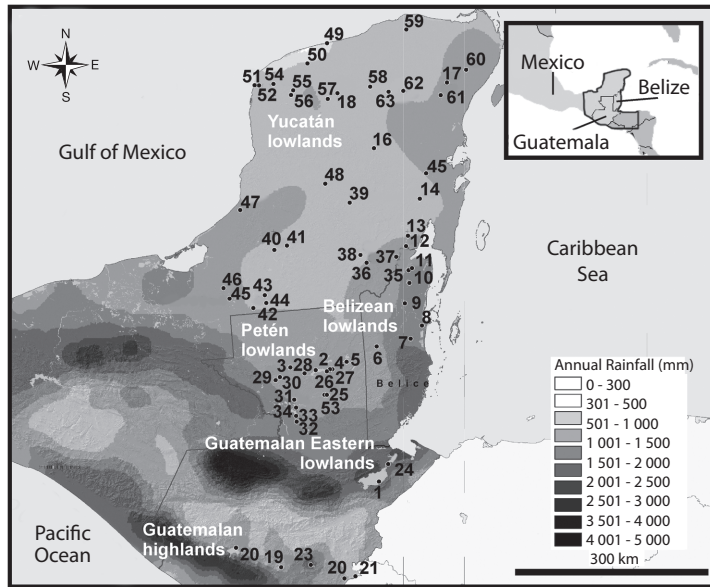
Consistent taxonomy, along with information on species autecology and the factors that affect species distributions and diversity, are indispensable to ensure that inferences from bioindicators, whether in modern or paleoenvironmental contexts, are valid. There have been few paleolimnological studies using bioindicators in remote tropical areas, in large part because of the paucity of autecological data. Detailed bioindicator analysis, coupled with information on physical and chemical attributes of aquatic ecosystems, is required to fully exploit the utility of such bioindicator taxa. These taxonomic groups are highly sensitive to environmental changes, such as shifts in salinity, conductivity or ionic concentration (Fritz *et al.* 1991, Smith 1993, Pérez *et al.* 2011b), total phosphorus concentration (Hausmann & Kienast 2006), lake level (Sylvestre 2002), air temperature (Walker *et al.* 1997, Brooks & Birks 2001), pH and organic matter concentration (Rosén *et al.* 2000), and changes in precipitation and trophic state (Massaferro *et al.* 2004, Pérez *et al.* 2010a).

There has been little research on the autecology of lacustrine organisms in the Northern Neotropics. Most studies have focused on taxonomy and biogeography. Studied groups include cladocerans (Elías-Gutiérrez *et al.* 2006, 2008) and copepods (Suárez-Morales & Elías-Gutiérrez 2000, Suárez-Morales & Reid 2003). Pérez *et al.* (2010a,b,c, 2011b) recently conducted studies on the freshwater ostracode fauna of the Yucatán Peninsula and surrounding areas. There are, however, few studies on diatoms and chironomids. This study presents information on chironomid, diatom, cladoceran, copepod and ostracode taxa from 63 waterbodies in the Northern Neotropics, along with associated environmental data. Our objective was to determine the factors that govern the distributions of these bioindicators so they could be used to infer late Quaternary environmental conditions and climate on the Yucatán Peninsula, Guatemala and Belize. In this study, we (1) present an inventory of the main species that inhabit aquatic ecosystems of the Northern Neotropics, (2) display ecological information from the studied waterbodies, (3) evaluate relationships between bioindicator relative abundances and environmental variables, (4) identify areas with high species richness and diversity that could be of conservation interest in this zoogeographic province and (5) develop a basis for transfer functions that can be applied in paleolimnological studies to infer past environmental variables such as water chemical composition and lake level. Ultimately, these transfer functions will be applied to fossil assemblages in long sediment cores retrieved from Lago Petén Itzá, Guatemala and other waterbodies in the Northern Neotropics to infer past environmental variables.

MATERIALS AND METHODS

Study site: The Yucatán Peninsula (Mexico, Guatemala and Belize, Fig. 1) and surrounding areas are rich in aquatic ecosystems that have different origins (tectonic, volcanic, karstic) and possess diverse water chemical composition. Chemical characteristics of waterbodies are mainly influenced by bedrock geology, climate and saltwater intrusion at coastal sites (Pérez *et al.* 2011a). The Yucatán Peninsula (Fig. 1) is a marine carbonate platform. The region is of interest to ecologists and paleoecologists alike, because it displays steep, increasing NW-S precipitation (~400-3 200mm/y) and altitude (~0-1 560m.a.s.l.) gradients (Pérez *et al.* 2011a). A dry season (January-May) and a rainy season (June-October) characterize the Yucatán Peninsula and surrounding areas. Short-duration showers

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Fig. 1. Map of the 63 sampled lakes, "cenotes", coastal waterbodies, rivers, wetland and ponds on the Yucatán Peninsula. Studied regions included the Guatemalan highlands, eastern lowlands, Petén lowlands, Belize lowlands and Yucatán lowlands. Full names, ID and ID-Nr. (number on this figure) of the sampled aquatic ecosystems can be found in tables 1a (lakes) and 1b ("cenotes", coastal lagoons, rivers, wetland and ponds). Gray scale shading indicates the steep, increasing NW-S precipitation gradient on the study area.

usually occur from November to December (Schmitter-Soto *et al.* 2002). Most of the study area is located in a dry tropical climate zone that is rich in aquatic ecosystems and displays high aquatic biodiversity (Lutz *et al.* 2000, Pérez *et al.* 2011a).

Sampling and habitat characterization: Two fieldtrips were carried out in the Yucatán Peninsula (Mexico), Guatemala and Belize (14°13'00''-21°25'00'' N and 87°20'00''-91°03'00'' W) in 2005-2006 and 2008. A single sampling was carried out for each lake. Chironomids, diatoms and microcrustaceans (cladocerans, copepods, ostracodes) were collected from 63 aquatic ecosystems (Fig. 1, Table 1a, b). These ecosystems included deep (10-340m) and shallow (<10m) lakes (Table 1a), "cenotes" (sinkholes), coastal lagoons, ponds, rivers, and wetlands (Table 1b). Surface sediment samples (lake deepest point, littoral zones, other water depths) were retrieved using an

Ekman grab. Ostracodes and cladocerans that live in macrophyte-rich littoral zones were collected with 250µm and 100µm-mesh hand nets, respectively. Physical and chemical variables and the chemical and isotopic composition of lake waters were studied to better characterize the habitat. Water samples were collected from at least three depths above the lake's deepest point (surface, mid-depth and bottom). Only surface waters near the shore were collected in smaller water bodies (ponds, rivers and wetlands). Water temperature, dissolved oxygen, pH and conductivity in surface waters were measured *in situ* using a WTW Multi Set 350i. Most measurements were done at midday. Water samples were collected in duplicate for laboratory analysis of Ca, Na, Mg, K, Cl, HCO_3, SO_4, and for $\delta^{18}O$ and $\delta^{13}C_{DIC}$ analysis. $\delta^{18}O$ values were used as an indicator of the balance between evaporation and precipitation and $\delta^{13}C$ values as a productivity proxy (Schwalb 2003). Cations were measured using

TABLE 1A

Location, morphometry and selected limnological variables of surface waters (single measurements) for sampled waterbodies on the Yucatán Peninsula (modified from Pérez *et al.* 2011b). ID indicates the abbreviations used for the studied waterbodies in figures 3-7. ID-Nr. indicates the location of all sampled aquatic ecosystems across a NW-S precipitation gradient in figure 1

Area	ID	ID-Nr.	Name of aquatic ecosystem	Coordinates N	W	Altitude [m.a.s.l]	Depth* [m]	Surface area [km²]	Temp. [°C]	Diss. oxygen [mg/L]	pH	Cond. [µS/cm]	Secchi [m]
Guatemalan Highlands	AMA	19	Amatitlán	14°26'03.7"	90°32'58.6"	1200	23	15.2	22.8	18.7	9.3	630	0.1-0.8
	ATI	20	Atitlán	14°42'34.8"	90°15'59.4"	1560	340	126	21.8	7.3	8.4	465	6.6
	AYA	23	Ayarza	14°25'39.3"	90°08'11.6"	1414	250	14	21.6	7.2	8.4	1772	11.4
	GÜI	21	Güija	14°15'43.7"	89°32'11.3"	433	21.5	45	26.2	7.7	8.4	206	1.4
	ATE	22	Atescatempa	14°13'01.1"	89°41'39.2"	587	2	1.1	27.3	6.7	8.0	283	0.1
Guatemalan Eastern Lowlands	IZA	1	Izabal	15°29'24.5"	89° 8'32.7"	4	14.8	645	26.4	7.6	8.3	215	–
Petén Lowlands	OQU	25	Oquevix	16°39'14.2"	89°44'26.1"	148	10	1.6	31.4	6.9	7.7	238	0.4
	SAL	26	Salpetén	16°58'38.2"	89°40'30.9"	114	38	2.9	29.7	8.4	8.2	4310	0.8
	MAC	4	Macanché	16°57'60.0"	89°38'06.5"	165	80	2.5	26.8	5.0	8.0	850	–
	YAX	5	Yaxhá	17°03'48.9"	89°24'27.1"	219	22	7	29.0	7.3	8.7	232	1.8
	ITZ	2	Petén Itzá	17°00'02.0"	89°51'16.4"	115	165	100	27.6	8.9	8.5	533	7.5
	SAC	28	Sacpuy	16°58'46.4"	90°00'52.2"	122	6	3.5	28.8	8.0	8.4	285	0.5
	PER	3	Perdida	17°04'00.7"	90°12'41.7"	75	4	11	28.8	9.8	8.8	232	0.7
	GLO	29	La Gloria	16°57'07.5"	90°22'36.1"	132	65	3.6	29.2	8.8	8.6	187	0.6
	DIE	30	San Diego	16°55'59.5"	90°24'54.5"	134	8.1	3.8	28.6	8.2	8.6	179	0.6
	POZ	32	Las Pozas	16°21'02.4"	90°10'28.9"	146	35	2.0	29.8	9.0	8.4	292	1.8
	PET	33	Petexbatún	16°26'11.8"	90°11'46.0"	115	40	5.6	30.9	9.7	8.0	568	0.6
	ROS	34	El Rosario	16°31'31.4"	90°09'36.2"	117	3	0.02	28.3	7.6	7.1	1019	–

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TABLE 1A (Continued)

Location, morphometry and selected limnological variables of surface waters (single measurements) for sampled waterbodies on the Yucatán Peninsula (modified from Pérez *et al.* 2011b). ID indicates the abbreviations used for the studied waterbodies in figures 3-7. ID-Nr. indicates the location of all sampled aquatic ecosystems across a NW-S precipitation gradient in figure 1

Area	ID	ID-Nr.	Name of aquatic ecosystem	Coordinates N W		Altitude [m.a.s.l]	Depth* [m]	Surface area [km²]	Temp. [°C]	Diss. oxygen [mg/L]	pH	Cond. [µS/cm]	Secchi [m]
Yucatán Lowlands	MIL	12	Milagros	18°30'41.5"	88°25'35.8"	1	4	3.1	27.9	12.4	8.1	2720	1.0
	BAC	13	Bacalar	18°39'54.0"	88°23'27.0"	1	16	51	27.0	7.9	7.8	1221	10.3
	NOH	14	Nohbec	19°08'8.54"	88°10'46.6"	1	0.6	8.5	29.2	9.4	8.5	1231	0.6
	OCO	15	Ocom	19°28'28.6"	88°03'17.9"	1	10	0.25	27.9	7.2	8.0	774	5.5
	CHI	16	Chichancanab	19°52'43.2"	88°46'06.5"	2	14	5.1	28.5	7.7	8.0	2060	2.8
	PUN	17	Punta Laguna	20°39'00.6"	87°38'28.2"	3	20	0.9	26.8	7.2	8.0	754	4.7
	JOS	36	San José Aguilar	18°22'04.5"	89°00'41.2"	107	3	2.0	–	4.8	8.0	488	0.6
	SAB	37	Sabanita	18°24'03.2"	88°34'20.6"	38	2.5	0.02	27.5	8.1	8.0	139	0.5
	BAT	38	Chacan-Bata	18°28'42.1"	89°05'13.9"	91	–	2.9	26.3	2.2	7.0	146	–
	LAR	39	Chacan-Lara	19°11'21.8"	88°10'17.0"	90	3	1.2	28.1	6.0	7.5	174	0.7
	JOB	41	Jobal	18°41'40.7"	90°06'45.4"	74	3		31.7	10.9	8.3	241	–
	FRA	42	San Francisco Mateos	17°53'55.9"	90°39'22.8"	52	5	0.1	24.8	0.9	7.3	474	–
	MIS	43	La Misteriosa	18°02'40.3"	90°29'14.0"	57	5.8	5.0	26.7	7.7	8.0	1411	2.1
	CAY	45	Cayucón	18°02'34.3"	90°58'33.0"	69	8	2.0	25.3	3.3	7.4	127	?
	YAL	18	Yalahau	20°39'25.9"	89°13'02.0"	2	11	0.25	28.8	8.7	8.9	2350	1.1
	COBA	61	Cobá	20°29'40.2"	87°44'19.2"	7	–	0.35	28.9	8.7	8.5	1213	0.9
Belizean Lowlands	ALM	8	Almond Hill Lagoon	17°27'49.0"	88°18'31.6"	1	1.9	1.5	27.5	6.4	7.1	1715	1.7
	CRO	9	Crooked Tree Lagoon	17°46'42.8"	88°31'37.4"	2	3.3	23	28.5	6.9	7.8	330	2.0
	HON	10	Honey Camp Lagoon	18°02'44.5"	88°26'20.5"	1	8	3.9	25.9	9.1	8.5	1481	1.8

* Maximum sampled water depth and/or maximum lake depth.

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TABLE 1B

Location, morphometry and selected limnological variables of surface waters (single measurements) for sampled "cenotes" (sinkholes), coastal waterbodies, rivers, wetlands and ponds on the Yucatán Peninsula (modified from Pérez et al. 2011b). ID indicates the abbreviations used for the studied waterbodies in figures 3-7. ID-Nr. indicates the location of all sampled aquatic ecosystems across a NW-S precipitation gradient in figure 1

Type of aquatic ecosystem	ID	ID-Nr.	Name	Coordinates N W	Altitude [m.a.s.l]	Depth* [m]	Surface area [km²]	Temp. [°C]	Diss. oxygen [mg/L]	pH	Cond. [µS/cm]	Secchi [m]
Cenotes	XLA	50	Xlacah	21°05'27.6" 89°35'53.3"	6	45	<0.01	27.9	4.0	7.0	1452	5
	MON	52	Petén de Monos	20°50'59.6" 90°19'13.8"	25	1.5	<0.01	26.6	1.4	6.9	3670	1.5
	IGN	55	San Ignacio Chochola	20°45'00.9" 89°50'03.2"	7	4	<0.01	27.4	2.7	6.9	2110	4
	CHE	56	Chenhá	20°41'23.0" 89°52'34.5"	3	2	<0.01	28.3	10.4	7.6	2520	3.5
	TIM	57	Timul	20°35'38.8" 89°21'23.7"	9	–	0.03	30.4	11.4	9.1	1465	0.2
	YOK	58	Yokdzonot	20°42'24.6" 88°43'52.0"	13	45	<0.01	25.2	5.3	7.4	949	7
	JUA	60	Juarez	20°48'09.6" 87°20'23.8"	14	25	0.03	27.9	8.7	8.1	643	1.6
	YAA	63	Ya'ax'ex	20°37'15.4" 88°24'56.0"	27	47	<0.01	26.4	10.6	8.0	793	0.8
	KAN	54	San Francisco Kana	20°51'22.2" 90°07'04.5"	3	–	0.01	30.7	9.7	8.2	1751	0.3
	TEK	62	Tekom	20°36'08.1" 88°15'52.5"	18	1.5	<0.01	25.5	6.7	7.3	958	1.5
Coastal water bodies	PRO	35	Progreso	18°13'05.2" 88°24'35.2"	5	3.2	7.2	26.4	7.0	8.2	2040	1.3
	CEN	11	Cenote Little Belize	18°13'36.9" 88°22'55.57"	7	11.1	0.06	25.8	8.3	8.2	5960	5.5
	ROSA	49	Rosada	21°20'11.3" 89°18'01.9"	4	0.5	2.3	28.1	10.5	8.7	55300	0.5
	CEL	51	Celestún	20°51'20.8" 90°22'39.2"	14	1.5	28	24.9	5.2	7.8	38200	0.5
Rivers	SUB	31	Subin	16°38'11.6" 90°11'00.3"	141	1	–	26.2	4.2	7.4	720	0.5
	IXL	27	Ixlú	16°58'27.3" 89°53'27.8"	110	1	–	25.9	6.7	7.5	1025	1
	DUL	24	Río Dulce	15°40'25.3" 88°57'49.3"	4	7	–	27.6	6.5	7.6	192	0.5
	CUB	44	Cuba	17°56'55.4" 90°28'39.1"	80	0.5	–	24.9	7.3	7.8	2040	0.5
	CAN	46	Candelaria	18°11'02.4" 91°02'59.6"	44	1.5	–	26.9	1.9	7.7	1564	1.0
	GUE	47	Guerrero	19°12'41.6" 90°43'47.6"	5	1	–	26.2	3.6	7.7	2700	0.5
Wetland	JAM	48	Jamolún	19°27'58.3" 89°29'45.1"	115	1.5	–	25.7	2.9	7.3	2520	0.5
Ponds	TÚM	53	Near Oquevix	16°40'31.7" 89°44'18.1"	179	1	<0.01	25.9	9.4	9.3	168	–
	LOC	59	Loché	21°25'04.3" 88°08'30.8"	20	1	<0.01	32.0	14.4	9.4	4340	0.2
	SIL	40	Silvituc	18°38'23.2" 90°17'35.2"	59	2.5	<0.01	30.2	7.7	8.2	183.2	–
	BZ1	6	Belize 1	17°14'33.5" 88°58'19.7"	77	1.5	<0.01	28.2	5.8	7.3	192	–
	BZ2	7	Belize 2	17°18'17.9" 88°29'18.9"	33	1	<0.01	27.4	7.5	8.0	244	–

* Maximum sampled water depth and/or maximum lake depth.

an ICP-OES Jobin Yvon JY 50 P Spectrometer. Bicarbonate was determined by titration with 0.1N HCl. Anions were measured using a 761 Compact IC Methrom at the Institut für Umweltgeologie, Technische Universität Braunschweig, Germany. Carbon and oxygen isotopes in waters were analyzed on a VG/Micromass PRISM Series II isotope ratio mass spectrometer and a Finnigan-MAT DeltaPlus XL isotope ratio mass spectrometer with a GasBench II universal on-line gas preparation device at the University of Florida, USA.

Bioindicator analysis: Surface sediments (~3g wet sediment) for chironomid analysis were (1) deflocculated in 10% KOH, (2) heated to 70°C for 10 minutes, (3) heated in water to 90°C for 20 minutes, and (4) sieved using 212µm and 95µm-mesh sieves. Chironomid head capsules were extracted from samples using a Bogorov sorting tray and fine forceps. Head capsules were slide-mounted in Euparal, identified, counted and photographed. Identification followed Pérez *et al.* (2010a). We identified taxa to the morphospecies level because taxonomic data are generally lacking for the Northern Neotropics.

Sediment samples for diatom analysis were treated with hot concentrated HNO_3, then with 33% H_2O_2, followed by successive rinsing and decanting with distilled water. Sub-samples of the homogenized solution were diluted by adding distilled water and were left to settle onto coverslips until dry. The coverslips were fixed onto glass slides with Naphrax® mountant (refraction index=1.73). Counting was performed generally on three slides using a Nikon NS600 microscope at 1000x magnification. The total number of valves counted per sample varied from 50 in nearly sterile samples to >1000 in rich samples. Diatom identification and taxonomy followed Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b) revised by the nomenclature of E. Fourtanier & J.P. Kociolek (on-line version of the Catalog of Diatom Names: http://research.calacademy.org).

Surface sediments were initially analyzed for cladocerans using low magnification on a light microscope. Remains were isolated, identified, and counted and specimens were kept in small vials filled with 3-4% formaldehyde solution. Several drops of glycerin were added to all vials to prevent desiccation. Permanent preparations of peculiar species were prepared for detailed microscopic observation to facilitate identification. We used polyvinyl lactophenol or Hydro-Matrix® as mounting media. Species were identified using the works of Korovchinsky (1992), Smirnov (1992, 1996), Lieder (1996), Flössner (2000), Kotov & Stifler (2006), Elías-Gutiérrez *et al.* (2008) and Van Damme *et al.* (2011). Calanoid copepods that live in open waters and littoral zones were sampled with a plankton net (100-µm mesh), preserved with 10% formalin, and identified and counted under a dissecting microscope. Literature used for taxonomic identification included Bowman (1996), Gutiérrez-Aguirre & Suárez-Morales (2000), Suárez-Morales & Elías-Gutiérrez (2000, 2001), and Elías-Gutiérrez *et al.* (2008). The details of the method used for ostracode analysis is in Pérez *et al.* (2011b). At least 100 adult ostracode valves were extracted from 50mL of wet surface sediment. Samples were wet-sieved using stacked sieves (630-, 250-, 63µm mesh). Both hard and soft parts were analyzed and used for identification to species level when possible. Identification followed Furtos (1933, 1936a, b), Brehm (1939), Keyser (1976), and Pérez *et al.* (2010a, b, c, 2011 b). Samples are stored at the Institut für Geosysteme und Bioindikation, Braunschweig, Germany. All bioindicator data are presented as relative abundances.

Species richness (S), i.e. the total number of species, and biodiversity, i.e. the Shannon Wiener Index (H) (Krebs 1989), were determined for each taxonomic group (chironomids, diatoms, cladocerans, copepods and ostracodes) in all waterbodies. Multivariate analysis was used to characterize species autecology by relating species relative abundances to water variables. Prior to statistical analysis, 14 environmental variables (water depth, water temperature, conductivity, dissolved oxygen (DO), pH, $\delta^{18}O$, $\delta^{13}C_{DIC}$, Ca, K, Mg, Na, Cl,

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HCO$_3$, SO$_4$) from all waterbodies were standardized (x-mean/st dev) and species relative abundances were log-transformed. Rare species, i.e. those present in <3 waterbodies, and samples containing few or no specimens, were excluded from analysis. Species included in the multivariate analysis are shown in bold in tables 2, 3 and 4. Thirty-eight chironomid, 97 diatom, 32 cladoceran, 3 copepod and 17 ostracode species were included in the statistical analysis. Correlations between environmental factors and the relative abundance of organisms were explored using Pearson correlation, which allowed up to seven environmental variables to be included in statistical analysis. Seven environmental variables were forward selected for statistical analysis of chironomids (DO, pH, temperature, conductivity, HCO$_3$, δ^{13}C, water depth) and diatoms (DO, pH, temperature, conductivity, δ^{13}C, δ^{18}O, water depth), four for cladocera (DO, temperature, HCO$_3$, conductivity), and six for copepods (temperature, HCO$_3$, Na, Cl, δ^{18}O, water depth) and ostracodes (temperature, pH, HCO$_3$, Na, conductivity, water depth). Forward selection of the environmental variables followed Hausmann & Kienast (2006) and Mischke et al. (2007).

Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were used to relate counts (relative abundance) of chironomids, diatoms, cladocerans and ostracodes to environmental variables, whereas Redundancy Analysis (RDA) was used for copepod counts. This was accomplished using Canoco for Windows 4.55 (Ter Braak & Šmilauer 2002). We first estimated the length of environmental gradients using a DCA and then used a CCA and RDA to discern the environmental factors that control bioindicator distributions in the study area. Generally, if a gradient is short (<3 SD), a linear model should be used, whereas with larger gradients (>4 SD), a unimodal model is recommended, because the approximation using the linear function is poor (Lepš & Šmilauer 2003).

RESULTS

We collected 66 chironomid species and morphospecies belonging to the subfamilies Chironominae, Orthocladiinae and Tanypodinae (Table 2), 282 diatom species that belong to the orders Centrales and Pennales (Table 3), 51 cladoceran species belonging to the orders Anompoda and Ctenopoda, six copepod species (Calanoida), and 29 ostracode species (Podocopina, Table 4). Photographs of selected species are shown in figure 2. Figures 3, 4, 5 and 6 display the relative abundances and altitude ranges of the aquatic bioindicators.

Chironomids: Figures 3 a, b, c display the relative abundances of the most common chironomid morphospecies, i.e. >10 individuals per waterbody and present in >2 aquatic ecosystems. The dominant tribe was Chironomini and consisted of 32 morphospecies (Table 2). Widely distributed taxa, i.e. present in >15 aquatic environments, included *Cladotanytarsus* sp.1, *Chironomus anthracinus*, *Cladopelma* sp., *Dicrotendipes* sp., *Goeldochironomus* sp., *Micropsectra* sp., *Parachironomus* sp., *Paratanytarsus* sp.1, *Polypedilum* sp. and *Polypedilum* sp. 2. *Chironomus anthracinus*, *Dicrotendipes* sp., *Goeldochironomus* sp. and *Labrundina* sp. had the highest relative abundances in most aquatic environments. Most chironomid species were collected at lower elevations (<450m a.s.l.). Only 15 species were collected in aquatic ecosystems in the Guatemalan highlands. Dominant species in highland lakes were *Apedilum* sp., *Apsectrotanypus* sp. and *Chironomus anthracinus*. *Chironomus anthracinus* dominated the chironomid community in hypereutrophic Lake Amatitlán, Southern Guatemala. Chironomids inhabiting mainly the Petén lowlands were *Stempellina* sp. and *Coelotanypus*/*Clinotanypus*. *Chironomus plumosus* was the dominant species in Progreso Lagoon, Belize, and *Cladopelma* sp. was collected in all studied aquatic ecosystems

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TABLE 2

Chironomids (family Chironomidae; n=66) found in aquatic ecosystems in the Northern Neotropics. Species are ordered alphabetically within subfamilies and tribes. Species codes in bold (n=38) were taxa included in multivariate analysis. Code indicates the species abbreviations used in Figures 3a,b,c and 8. A number or letter was designated along with the genus to identify different morphospecies. For the ecosystem studies see tables 1A, B

Taxa	Code	Taxa	Code
Subfamily Chironominae		*Cladotanytarsus* sp.2	CLA2
Tribe Chironomini		*Micropsectra* sp.	**MICR**
Apedilum sp.	**APED**	Tanytarsini A	**TANA**
Axarus sp.	AXAR	Tanytarsini C	**TANC**
Beardius sp.	**BEAR**	Tanytarsini D	**TAND**
Brundinella sp.	BRUN	Tanytarsini F	TANF
Chironomus anthracinus Zetterstedt 1860	**CHAN**	Tanytarsini J	**TANJ**
Chironomus plumosus Linnaeus 1758	**CHPL**	Tanytarsini K	TANK
Cladopelma sp.	**CLAD**	*Paratanytarsus* sp.1	**PAR1**
Corynocera ambigua Zetterstedt 1838	**CORC**	*Paratanytarsus* sp.2	**PAR2**
Corynocera olivieri type	CORO	**Tribe Pseudochironomini**	
Cryptochironomus sp.	CRYP	*Pseudochironomus* sp.	**PSEU**
Dicrotendipes sp.	**DICR**	**Subfamily Orthocladiinae**	
Einfeldia sp.	EINF	*Corynoneura* sp.	**CORY**
Endochironomus sp.	**ENDO**	*Cricotopus* spp.	**CRIC**
Endotribelos sp.	**ENTR**	*Eukiefferiella* sp.	EUKI
Glyptotendipes sp.1	GLEN	*Limnophies* sp.	LIMN
Glyptotendipes sp.2	**GLYP**	*Mesosmittia* sp.	MESS
Goeldochironomus sp.	**GOEL**	*Parakiefferiella fennica* Tuiskunen 1986	PAFE
Harrisius sp.	HARR	*Parapsectrocladius* sp.	PAPS
Kiefferulus sp.	KIEF	*Pseudosmittia* sp.	PSSM
Lauternborniella sp.	**LAUT**	*Psectrocladius* sp.	PSEC
Paracladopelma sp.	PCLA	**Subfamily Tanypodinae**	
Paratendipes sp.	PART	*Ablabesmya* sp.	**ABLA**
Parachironomus sp.	**PCHI**	*Alotanypus* sp.	ALOT
Phaenopsectra sp.	PHAE	*Apsectrotanypus* sp.	**APSE**
Polypedilum sp.	**POLY**	*Coelotanypus/Clinotanypus*	**COEL**
Polypedilum sp.2	**PO16**	*Djalmabatista* sp.	**DJAL**
Sergentia sp.	SERG	*Fittkauimyia* sp.	FITT
Stempellina sp.	**STEM**	*Labrundina* sp.	**LABR**
Saetheria sp.	SAET	*Larsia* sp.	**LARS**
Stenochironomus sp.	**STEN**	*Macropelopia/Apsectrotanypus*	**MACR**
Sublettea sp.	SUBL	*Monopelopia* sp.	MONO
Xenochironomus sp.	XENO	*Procladius* sp.	**PROC**
Tribe Tanytarsini		Tanypodinae indet.	**TAID**
Cladotanytarsus sp.1	**CLA1**	*Zavrelymia* sp.	ZAVR

TABLE 3

Diatom species (n=282) found in aquatic ecosystems in the Northern Neotropics. Species are ordered alphabetically within classes, orders, suborders and families. Species codes in bold (n=97) were included in multivariate analysis. Code indicates the species abbreviations used in figures 4a,b and 8. A number was designated along with the genus to identify different morphospecies. For the ecosystem studies see tables 1a,b

Taxa	Code	Taxa	Code
Class Bacillariophyceae		**Order Pennales**	
Order Centrales		**Sub-Order Araphidineae**	
Sub-Order Coscinodiscineae		**Fragilariaceae**	
Hemidiscaceae		*Campylostylus normannianus* (Greville) Gerloff, Natour & Rivera 1978	CAPS
Actinocyclus sp.	ACTI	*Cymatosira lorenziana* Grunow 1862	CLOZ
Melosiraceae		*Fragilaria bidens* Heiberg 1863	FRBI
Hyalodiscus scoticus (Kützing) Grunow 1879	HYSC	*Fragilaria capucina* Desmazieres emend Lange-Bertalot 1980	FCA
Paraliaceae		*Fragilaria capucina* var. *vaucheriae* (Kützing) Lange-Bertalot 1980	FCAV
Paralia sulcata (Ehrenberg) Cleve 1873	PARA	*Fragilaria crotonensis* Kitton 1869	FCR
Thalassiosiraceae		*Fragilaria famelica* (Kützing) Lange-Bertalot 1980	FF
Aulacoseira ambigua (Grunow) Simonsen 1979	MA	*Fragilaria tenera* (W. Smith) Lange-Bertalot 1980	FT
Aulacoseira crenulata (Ehrenberg) Thwaites 1848	AUC	*Fragilaria ulna* var. *goulardi* (Brébisson) Lange-Bertalot 1980	FRGO
Aulacoseira distans (Ehrenberg) Simonsen 1979	MD	*Opephora marina* (Gregory) Petit 1888	OMAR
Aulacoseira granulata (Ehrenberg) Simonsen 1979	MG	*Pseudostaurosira brevistriata* (Grunow in Van Heurck) Williams & Round 1987	FBR
Aulacoseira granulata var. *angustissima* (Otto Müller) Simonsen 1979	MGA	*Staurosira construens* Ehrenberg 1843	FRAC
Aulacoseira granulata f. *curvata* (Hustedt) Simonsen 1979	MGC	*Staurosirella pinnata* (Ehrenberg) Williams & Round 1987	FP
Cyclotella atomus Hustedt 1937	CYAT	*Synedra hartii* Cholnoky 1963	FHA
Cyclotella caspia Grunow 1878	CCAS	*Tabularia tabulata* (C.A.Agradh) Snoeijs 1992	TABA
Cyclotella comensis Grunow in Van Heurck 1882	CYCO	*Tabularia fasciculata* (C.A.Agradh) Williams & Round 1986	TAFA
Cyclotella cyclopuncta Håkansson & Carter 1990	CYCL	*Ulnaria acus* (Kützing) Aboal in Aboal, Alvarez-Cobelas, Cambra & Ector 2003	SYNA
Cyclotella meneghiniana Kützing 1844	CYMG	*Ulnaria delicatissima* var. *angustissima* (Grunow in Van Heurck) Aboal in Aboal, Alvarez Cobelas, Cambra & Ector 2003	FAAU
Cyclotella striata (Kützing) Grunow in Cleve & Grunow 1880	CYST	*Ulnaria delicatissima* var. *angustissima* (Grunow in Van Heurck) Aboal in Aboal, Alvarez-Cobelas, Cambra & Ector 2003	FARD
Cyclotella aff. *petensis*	CYEN		
Cyclotella aff. *striata*	CAST	*Ulnaria ulna* (Nitzsch) Compère 2001	SYNU
Cyclotella sp.	CPS	**Sub-Order Raphidineae**	
Cyclotella sp. 22	CP22	**Eunotiaceae**	
Discostella pseudostelligera (Hustedt) Houk & Klee 2004	CCP	*Eunotia camelus* Ehrenberg 1841	EUCM
Discostella aff. *pseudostelligera*	CYAP	*Eunotia bilunaris* (Ehrenberg) Mills 1933-1935	EUL
Discostella stelligera (Cleve et Grunow) Houk & Klee 2004	CYCS	*Eunotia monodon* Ehrenberg 1841(1843)	EUMO
Stephanodiscus hantzschii Grunow in Cleve & Grunow 1880	STHA	*Eunotia praerupta* Ehrenberg 1841(1843)	EUPR
Stephanodiscus minutulus (Kützing) Cleve & Möller 1882	STME	*Eunotia* sp.	EUSP
Stephanodiscus medius H. Håkansson 1986	STNU	*Peronia fibula* (Brébisson in Kützing) Ross 1956	PERF
Stephanodiscus parvus Stoermer & Håkansson 1984	STPA		
Thalassiosira sp.	THAS		
Sub-Order Rhizosoleniineae			
Biddulphiaceae			
Terpsinoe musica Ehrenberg 1843	TERM		

TABLE 3 (Continued)
Diatom species (n=282) found in aquatic ecosystems in the Northern Neotropics. Species are ordered alphabetically within classes, orders, suborders and families. Species codes in bold (n=97) were included in multivariate analysis. Code indicates the species abbreviations used in figures 4a,b and 8. A number was designated along with the genus to identify different morphospecies. For the ecosystem studies see tables 1a,b

Taxa	Code	Taxa	Code
Achnanthaceae		*Brachysira* sp.	BRSP
Achnanthes minutissima var. *scotica* (Carter) Lange-Bertalot in Lange-Bertalot & Krammer 1989	**AMSC**	*Caloneis alpestris* (Grunow) Cleve 1894	CAL
Achnanthidium brevipes (Agardh) Heiberg 1863	ABR	*Caloneis bacillum* (Grunow) Cleve 1894	CAB
Achnanthidium exiguum (Grunow) Czarnecki 1994	AEX	*Caloneis fontinalis* (Grunow) Lange-Bertalot & Reichardt in Lange-Bertalot & Metzeltin 1996	CAFO
Achnanthidium hungaricum Grunow 1863	AHU	*Capartogramma paradisiaca* Novelo, Tavera & Ibarra 2007	**CAPA**
Achnanthidium minutissimum (Kützing) Czarnecki 1994	AMI	*Climaconeis colemaniae* A.K.S.K. Prasad in Prasad, A.K.S.K., Riddle, K.A. & J.A. Nienow 2000	CLIM
Cocconeis neodiminuta Krammer 1990	CD	*Craticula ambigua* (Ehrenberg) Mann in Round, Crawford & Mann 1990	CRAA
Cocconeis placentula Ehrenberg 1838	CP	*Craticula cuspidata* (Kützing) Mann in Round, Crawford & Mann 1990	NCU
Karayevia submarina (Hustedt) Bukhtiyarova 2006	ASUB	*Craticula halophila* (Grunow ex Van Heurck) Mann in Round, Crawford & Mann 1990	**NAHA**
Psammothidium marginulatum (Grunow) Bukhtiyarova et Round 1996	AUM	*Craticula perrotettii* Grunow 1867	CRPE
Naviculaceae		*Cymbella mexicana* (Ehrenberg) Cleve 1984	CYMX
Amphipleura pellucida (Kützing) Kützing 1844	APLL	*Cymbella rhomboidea* Boyer 1916	CYRH
Amphora arenaria Donkin 1858	AMRE	*Cymbella* sp. 25	CY25
Amphora arenicola Grunow in Cleve 1895	AMER	*Diadesmis confervacea* Kützing 1844	NACF
Amphora copulata (Kützing) Schoeman & Archibald 1986	AMPU	*Diadesmis contenta* (Grunow ex Van Heurck) Mann in Round, Crawford & Mann 1990	NCN
Amphora cymbifera Gregory 1857	AMCY	*Encyonema densistriata* Novelo, Tavera & Ibarra 2007	ENDE
Amphora graeffeana Hendey 1973	AMGR	*Encyonema gracile* Rabenhorst 1853	CYL
Amphora granulata Gregory 1857	APTA	*Encyonema mesianum* (Cholnoky) Mann in Round, Crawford & Mann 1990	CYME
Amphora holsaticoides Nagumo & Kobayasi 1990	AMHS	*Encyonema minutum* (Hilse in Rabenhorst) Mann in Round, Crawford & Mann 1990	CYMT
Amphora lybica Ehrenberg 1840	AY	*Encyonema muelleri* (Hustedt) Mann in Round, Crawford & Mann 1990	CYMU
Amphora marina W. Smith 1857	AMAR	*Encyonema perpusillum* (A. Cleve) Mann in Round, Crawford & Mann 1990	CYPE
Amphora pediculus (Kützing) Grunow in Schmidt *et al.* 1875	AMPE	*Encyonema silesiacum* (Bleisch in Rabenhorst) Mann in Round, Crawford & Mann 1990	**CYML**
Amphora proteus Gregory 1857	AMP	*Encyonema turgidum* (Gregory) Grunow in Schmidt et al. 1875	CYTI
Amphora securicula Peragallo & Peragallo 1899	AMSE	*Encyonopsis angusta* Krammer et Lange-Bertalot in Krammer 1997	CYAM
Anomoeoneis sphaerophora Pfitzer 1871	ANS	*Encyonopsis cesatii* (Rabenhorst) Krammer 1997	CYC
Anomoeoneis sphaerophora f. *costata* (Kützing) A.-M. Schmid 1977	ANSC	*Encyonopsis falaisensis* (Grunow) Krammer 1997	CYF
Anomoeoneis sphaerophora f. *sculpta* (Ehrenberg) Krammer in Krammer & Lange-Bertalot 1985	ANSS	*Encyonopsis microcephala* (Grunow) Krammer 1997	CYMI
Anomoeoneis vitrea (Grunow) Ross in Patrick & Reimer 1966	ANV	*Encyonopsis naviculacea* (Grunow) Krammer 1997	CYNV
Brachysira australofollis H. Lange-Bertalot & G. Moser 1994	BRAL	*Diploneis caffra* (Giffen) A. Witkowski, H. Lange-Bertalot & D. Metzeltin 2000	DICA
Brachysira hofmanniae H. Lange-Bertalot in H. Lange-Bertalot & G. Moser 1994	BROF	*Diploneis fusca* (Gregory) Cleve 1894	DFUS
Brachysira neoexilis H. Lange-Bertalot in H. Lange-Bertalot & G. Moser 1994	**BREX**		
Brachysira procera H. Lange-Bertalot & G. Moser 1994	**BRPR**		
Brachysira vitrea (Grunow) R. Ross in Hartley 1986	BRVI		

TABLE 3 (Continued)
Diatom species (n=282) found in aquatic ecosystems in the Northern Neotropics. Species are ordered alphabetically within classes, orders, suborders and families. Species codes in bold (n=97) were included in multivariate analysis. Code indicates the species abbreviations used in figures 4a,b and 8. A number was designated along with the genus to identify different morphospecies. For the ecosystem studies see tables 1a,b

Taxa	Code	Taxa	Code
Diploneis litoralis (Donkin) Cleve 1894	DILI	*Mastogloia asperuloides* Hustedt 1933	MAAS
Diploneis oblongella (Naegeli in Kutzing) Cleve-Euler in Cleve-Euler (& Osvald) 1922	DOB	*Mastogloia braunii* Grunow 1863	MABR
Diploneis ovalis (Hilse in Rabenhorst) Cleve 1891	DO	*Mastogloia constricta* Cleve 1892	MACO
Entomoneis paludosa (W. Smith) Reimer in Patrick & Reimer 1975	ENTO	*Mastogloia cyclops* Voigt 1942	MACY
Eolimna minima (Grunow in Van Heurck) H. Lange-Bertalot in G. Moser, H. Lange-Bertalot & D. Metzeltin 1998	NAI	*Mastogloia elliptica* (Agardh) Cleve in Schmidt *et al.* 1893	MASE
Eolimna submuralis (Hustedt) Lange-Bertalot & Kulikovskiy in Kulikovskiy *et al.* 2010	NAS	*Mastogloia elliptica* var. *dansei* (Thwaites) Cleve 1895	MDAN
Eolimna aff. *submuralis* (Hustedt) Lange-Bertalot & Kulikovskiy in Kulikovskiy *et al.* 2010	NUSI	*Mastogloia lanceolata* Thwaites in W. Smith 1856	MLAN
Fallacia pygmaea (Kützing) Stickle & Mann in Round, Crawford & Mann 1990	NPYG	*Mastogloia malayensis* Hustedt 1942	MALY
Fistulifera pelliculosa (Brebisson) Lange-Bertalot 1997	NPE	*Mastogloia pseudoelegans* Hustedt 1955	MELP
Gomphonema affine Kützing 1844	GAFF	*Mastogloia pusilla* Grunow 1878	MAPP
Gomphonema amoenum Lange-Bertalot in Krammer & Lange-Bertalot 1985	GOE	*Mastogloia recta* Hustedt 1942	MREC
Gomphonema angustum Agardh 1831	GOIM	*Mastogloia smithii* Thwaites in lit. ex W. Smith 1856	MASM
Gomphonema clevei Fricke in Schmidt *et al.* 1902	GC	*Mastogloia smithii* var. *lacustris* Grunow 1878	MASL
Gomphonema gracile Ehrenberg 1854	GG	*Mastogloia* aff. *gracilis* Hustedt 1933	MAAG
Gomphonema hebridense Gregory 1854	GOH	*Mastogloia* aff. *recta* Hustedt 1942	MARC
Gomphonema insigne Gregory 1856	GOIN	*Mastogloia* sp.	MASP
Gomphonema parvulum (Kützing) Kützing 1849	GP	*Navicula apta* Hustedt 1955	NAPT
Gomphonema pseudoaugur Lange-Bertalot 1979	GPA	*Navicula concentrica* Carter & Bailey-Watts 1981	NCCA
Gomphonema pseudotenellum Lange-Bertalot in Krammer & Lange-Bertalot 1985	GPST	*Navicula cryptotenella* Lange-Bertalot in Krammer & Lange-Bertalot 1985	NRT
Gomphonema truncatum Ehrenberg 1832	GT	*Navicula eidrigiana* Carter 1979	NEDR
Gomphonema vibrioides Reichardt & Lange-Bertalot 1991	GOVI	*Navicula flanatica* Grunow 1860	NAFN
Gomphonema aff. *bozenae* Lange-Bertalot et Reichardt in Lange-Bertalot & Metzeltin 1996	GOBE	*Navicula gregaria* Donkin 1861	NGG
Gomphonema sp.	GOSP	*Navicula hasta* Pantocsek 1892	NHAS
Gyrosigma baltica (Ehrenberg) Rabenhorst 1853	GBAL	*Navicula leptostriata* Jørgensen 1948	NLEP
Halamphora acutiuscula (Kützing) Z. Levkov 2009	AMCU	*Navicula palestinae* Gerloff, Natour & Rivera 1984	NPAE
Halamphora coffeaeformis (Agardh) Z. Levkov 2009	AMCO	*Navicula perminuta* Grunow in Van Heurck 1880	NAPR
Halamphora montana (Krasske) Z. Levkov 2009	AMMO	*Navicula phyllepta* Kützing 1844	NAPH
Halamphora normanii (Rabenhorst) Z. Levkov 2009	AMNI	*Navicula pseudoarvensis* Hustedt 1942	NPS
Halamphora veneta (Kützing) Z. Levkov 2009	AMVN	*Navicula pseudocrassirostris* Hustedt 1961	NPCO
Hippodonta capitata (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski 1996	NACA	*Navicula radiosa* Kützing 1844	NRA
		Navicula salinarum Grunow 1880	NRUM
Hippodonta hungarica (Grunow) Lange-Bertalot, Metzeltin & Witkowski 1996	NCHU	*Navicula salinicola* Hustedt 1939	NASA
		Navicula schroeteri Meister 1932	NACH
		Navicula subrhynchocephala Hustedt 1935	NCHO
		Navicula subrostellata Hustedt 1955	NSRO
		Navicula subrotundata Hustedt 1945	NSO
		Navicula veneta Kützing 1844	NAVE
		Navicula sp.	NS
Luticola mutica (Kützing) Mann in Round, Crawford & Mann 1990	NAMM	*Neidium ampliatum* (Ehrenberg) Krammer in Krammer & Lange-Bertalot 1985	NEAP
		Neidium iridis (Ehrenberg) Cleve 1894	NEI
		Oestrupia powelli (Lewis) Heiden ex Hustedt 1935	NPOW

TABLE 3 (Continued)
Diatom species (n=282) found in aquatic ecosystems in the Northern Neotropics. Species are ordered alphabetically within classes, orders, suborders and families. Species codes in bold (n=97) were included in multivariate analysis. Code indicates the species abbreviations used in figures 4a,b and 8. A number was designated along with the genus to identify different morphospecies. For the ecosystem studies see tables 1a,b

Taxa	Code	Taxa	Code
Parlibellus panduriformis John 1991	PARP	*Stauroneis schimanskii* Krammer in Krammer & Lange-Bertalot 1985	STSH
Parlibellus aff. *crucicula* (W. Smith) A. Witkowski, H. Lange-Bertalot & D. Metzeltin 2000	NCRU	*Stauroneis* aff. *schimanskii* Krammer in Krammer & Lange-Bertalot 1985	STAH
Parlibellus sp.	PARL	**Epithemiaceae**	
Petroneis sp.	PETRO	*Epithemia adnata* (Kützing) Brébisson 1838	EZ
Pinnularia acrosphaeria Rabenhorst 1853	PA	*Epithemia turgida* (Ehrenberg) Kützing 1844	ET
Pinnularia alpina Mereschkowsky 1906	PIAL	*Epithemia* sp.	EPSP
Pinnularia appendiculata (Agardh) Cleve 1895	PIAP	*Rhopalodia acuminata* Krammer in Lange-Bertalot & Krammer 1987	RHAC
Pinnularia borealis Ehrenberg 1843	PIB	*Rhopalodia gibba* (C.G. Ehrenberg 1830) O. Muller 1895	RG
Pinnularia braunii (Grunow in Van Heurck) Cleve 1895	PBR	**Bacillariaceae**	
Pinnularia cuneatiformis Krammer et Metzeltin in Metzeltin & Lange-Bertalot 1998	PICU	*Bacillaria paxillifera* (O. F. Müller) Hendey 1951	BACX
Pinnularia divergens W. Smith 1853	PIDI	*Denticula elegans* Kützing 1844	DE
Pinnularia interrupta W. Smith 1853	PIIT	*Denticula kuetzingii* Grunow 1862	DKU
Pinnularia major (maior) (Kützing) Rabenhorst 1853	PIMA	*Denticula neritica* Holmes & Croll 1984	DNER
Pinnularia mesolepta (Ehrenberg) W. Smith 1853	PIME	*Denticula subtilis* Grunow 1862	DSB
Pinnularia microstauron (Ehrenberg) Cleve 1891	PIMI	*Hantzschia amphioxys* (Ehrenberg) Grunow in Cleve & Grunow 1880	HA
Pinnularia subcapitata Gregory 1856	PISU	*Hantzschia virgata* (Roper) Grunow in Cleve & Grunow 1880	HAVR
Pinnularia tabellaria Ehrenberg 1843	PITB	*Nitzschia acidoclinata* Lange-Bertalot 1976	NIAC
Pinnularia stomatophora (Grunow in Schmidt *et al.*) Cleve 1895	PITO	*Nitzschia amphibia* Grunow 1862	NIAM
Pinnularia streptoraphe Cleve 1891	PITR	*Nitzschia amphibia* f. *frauenfeldii* (Grunow) Lange-Bertalot in Lange-Bertalot & Krammer 1987	NIFE
Placoneis clementioides (Hustedt) Cox 1987	PLCI	*Nitzschia amphibioides* Hustedt 1942	ND
Placoneis porifera (Hustedt) E.J. Cox 2003	NPOR	*Nitzschia bacillum* Hustedt 1922	NIBU
Plagiotropis neovitrea Paddock 1988	PLVI	*Nitzschia commutata* Grunow in Cleve & Grunow 1880	NTCM
Pleurosigma sp.	PLSP	*Nitzschia constricta* (Kützing) Ralfs in Pritchard 1861	NICO
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot 1980	GAB	*Nitzschia distans* Gregory 1857	NDIN
Sellaphora densistriata (H. Lange-Bertalot & D. Metzeltin) H. Lange-Bertalot & D. Metzeltin in D. Metzeltin & H. Lange-Bertalot 2002	SEDE	*Nitzschia frustulum* (Kützing) Grunow in Cleve & Grunow 1880	NFRU
Sellaphora laevissima (Kützing) D.G. Mann 1989	NAV	*Nitzschia frustulum* var. *bulnheimiana* (Rabenhorst; Rabenhorst) Grunow in Van Heurck 1881	NBUL
Sellaphora pupula (Kützing) Mereschkowsky 1902	NAPP	*Nitzschia gessneri* Hustedt 1953	NGSS
Sellaphora seminulum (Grunow) D.G. Mann 1989	NSM	*Nitzschia gracilis* Hantzsch 1860	NTGR
Sellaphora stroemii (Hustedt) H. Kobayasi in Mayama, S., Idei, M., Osada, K. & T. Nagumo 2002	NSTR	*Nitzschia granulata* Grunow 1880	NGRA
Seminavis strigosa (Hustedt) D.G. Mann & A. Economou-Amilii in D.B. Danielidis & D.G. Mann 2003	AMST	*Nitzschia grossestriata* Hustedt 1955	NIGR
		Nitzschia hantzschiana Rabenhorst 1860	NIH
Seminavis robusta Danielidis & D.G. Mann 2002	SEMI	*Nitzschia homburgiensis* Lange-Bertalot 1978	NIHO
Seminavis pusilla (Grunow) E.J. Cox & G. Reid 2004	CYMP	*Nitzschia inconspicua* Grunow 1862	NI
Stauroneis anceps Ehrenberg 1843	SA	*Nitzschia lacuum* Lange-Bertalot 1980	NILA
Stauroneis nana Hustedt 1957	STNA	*Nitzschia liebethruthii* Rabenhorst 1864	NILI
Stauroneis phoenicenteron (Nitzsch) Ehrenberg 1843	SPH	*Nitzschia linearis* (Agardh) W. Smith 1853	NILN

TABLE 3 (Continued)
Diatom species (n=282) found in aquatic ecosystems in the Northern Neotropics. Species are ordered alphabetically within classes, orders, suborders and families. Species codes in bold (n=97) were included in multivariate analysis. Code indicates the species abbreviations used in figures 4a,b and 8. A number was designated along with the genus to identify different morphospecies. For the ecosystem studies see tables 1a,b

Taxa	Code	Taxa	Code
Nitzschia littorea Grunow in Van Heurck 1881	NIL	*Tryblionella acuminata* W. Smith 1853	NICU
Nitzschia microcephala Grunow 1880	NIMI	*Tryblionella hungarica* (Grunow) Mann in Round, Crawford & Mann 1990	NIHU
Nitzschia miserabilis Cholnoky 1963	NBIS		
Nitzschia nana Grunow in Van Heurck 1881	NINA	*Tryblionella levidensis* W. Smith 1856	NILE
Nitzschia palea (Kützing) W. Smith 1856	NPA	*Tryblionella panduriformis* (Gregory) Pelletan 1889	NPAN
Nitzschia pararostrata (Lange-Bertalot) Lange-Bertalot 1996	NIPR	*Tryblionella scalaris* (Ehrenberg) P. Siver & P.B. Hamilton 2005	NSCI
Nitzschia perminuta (Grunow in Van Heurck) M. Peragallo 1903	NIPE	**Surirellaceae**	
		Campylodiscus echeneis Ehrenberg ex Kützing 1844	CAEC
Nitzschia pseudofonticola Hustedt 1942	NIPF	*Campylodiscus clypeus* (Ehrenberg) Kützing 1844	CAMPY
Nitzschia sigma (Kützing) W. Smith 1853	NSIG	*Stenopterobia delicatissima* (Lewis) Van Heurck 1896	SUE
Nitzschia sp. 1	NISP1	*Surirella (Suriraya) elegans* Ehrenberg 1843	SUEL
Nitzschia subacicularis Hustedt *in* Schmidt *et al.* 1922	NISU	*Surirella ovalis* Brébisson 1838	SUO
Nitzschia thermaloides Hustedt 1955	NTOI	*Surirella* sp.	SUR
Nitzschia vitrea Norman 1861	NIVT	*Surirella striatula* Turpin 1816-1829	SUTR

TABLE 4

Microcrustaceans found in aquatic ecosystems in the Northern Neotropics. Species are ordered alphabetically within orders and families. Species codes in bold (cladocerans= 32; copepods= 3; ostracodes=17) were included in multivariate analysis. Code indicates the species abbreviations used in figures 6 and 8. For the ecosystem studies see tables 1a,b
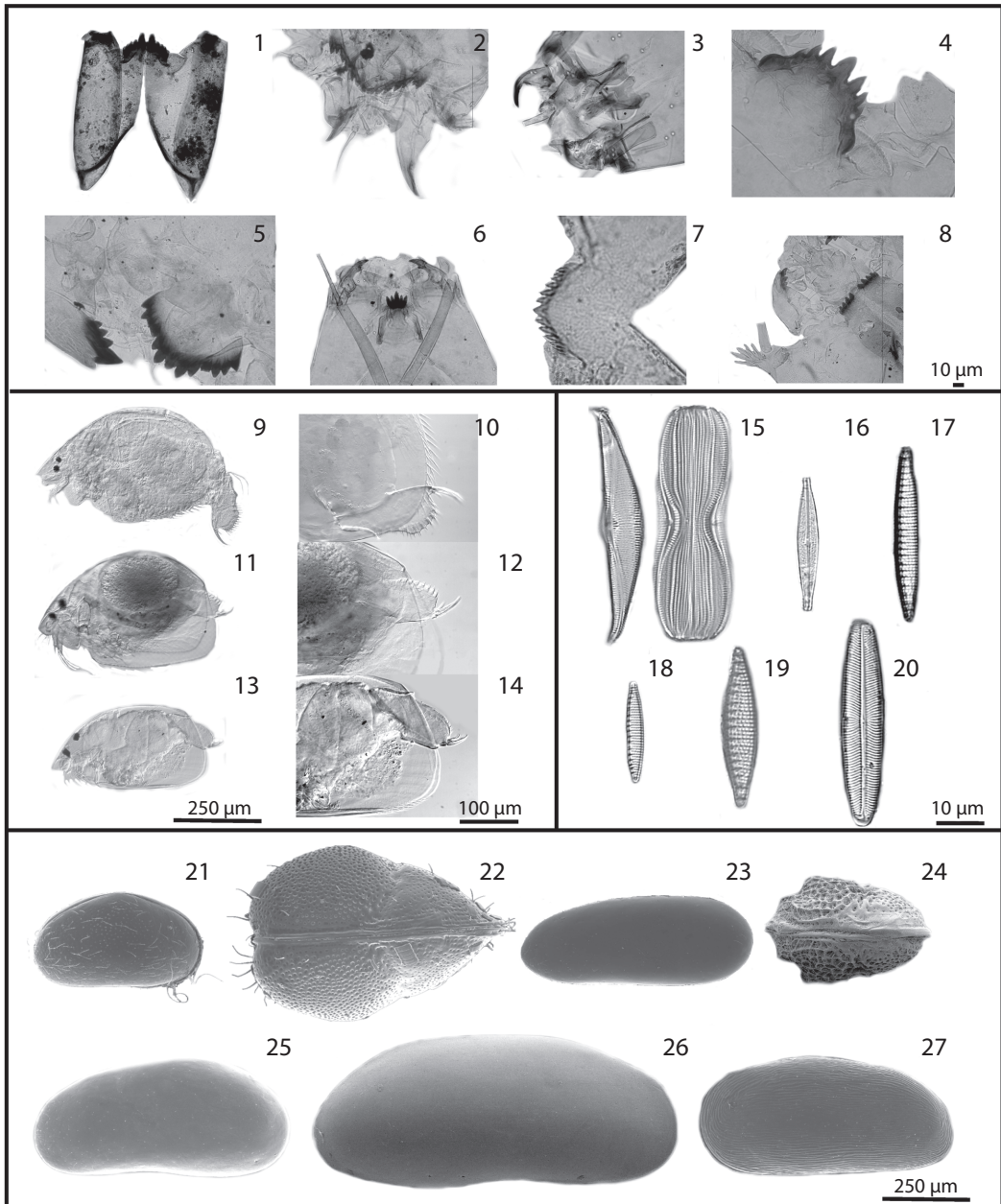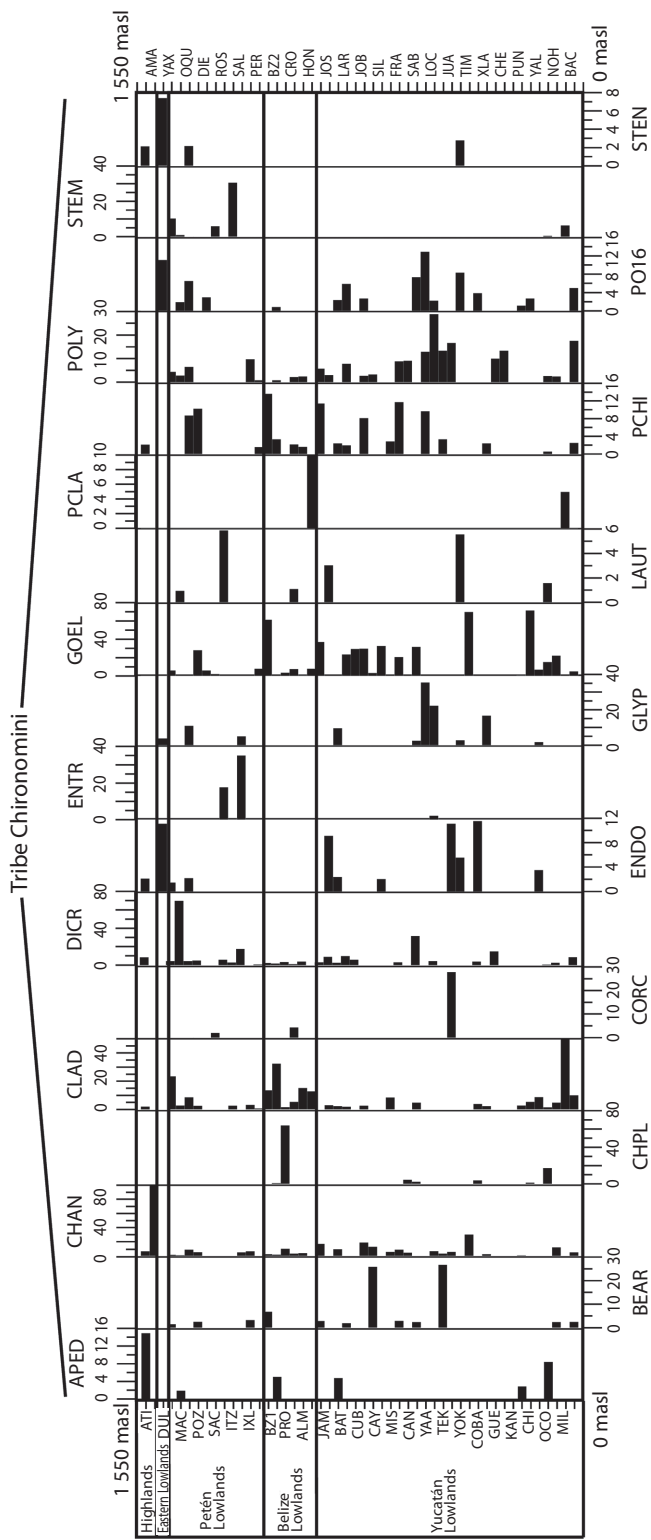
Taxa	Code	Taxa	Code
Cladocerans (n=51)		*Bosminopsis deitersi* Richard 1895	BDE
Order Ctenopoda		**Family Ilyocryptidae**	
Family Sididae		*Ilyocryptus spinifer* Herrick 1882	ISP
Diaphanosoma brevireme Sars 1901	DBR	**Family Macrothricidae**	
Latonopsis australis group	LAU	*Macrothrix elegans* Sars 1901	MEL
Pseudosida ramosa Daday 1904	PRA	*Macrothrix paulensis* (Sars 1900)	MPA
Order Anomopoda		*Macrothrix* cf. *spinosa* King 1853	MSP
Family Daphniidae		*Streblocerus pygmaeus* Sars 1901	SPY
Ceriodaphnia dubia Richard 1894	CDU	**Family Chydoridae**	
Ceriodaphnia cf. *rigaudi* Richard 1894	CRI	*Alona dentifera* (Sars 1901)	ADE
Daphnia mendotae Birge 1918	DME	*Alona guttata* group	AGU
Daphnia pulicaria Forbes 1893	DPU	*Alona ossiani* Sinev 1998	AOS
Scapholeberis armata freyi Dumont & Pensaert 1983	SAR	*Alonella* cf. *excisa* (Fischer, 1854)	AEX
Simocephalus congener (Koch 1841)	SCO	*Anthalona brandorffi* (Sinev & Hollwedel 2002)	ABR
Simocephalus mixtus Sars 1903	SMI	*Anthalona verrucosa* (Sars 1901)	AVE
Simocephalus serrulatus (Koch 1841)	SSE	*Camptocercus dadayi* Stingelin 1900	CDA
Family Moinidae		*Chydorus brevilabris* Frey 1980	CHB
Moina minuta Hansen 1899	MMI	*Chydorus eurynotus* Sars 1901	CHE
Moinodaphnia macleayi (King 1953)	MMA	*Chydorus nitidulus* Sars 1901	CHN
Family Bosminidae		*Coronatella circumfimbriata* (Megard 1967)	CCI
Bosmina huaronensis Delachaux 1918	BHU	*Coronatella monacantha* (Sars 1901)	CMO
Bosmina tubicen Brehm 1953	BTU	*Dadaya macrops* (Daday 1888)	DMA

TABLE 4 (Continued)
Microcrustaceans found in aquatic ecosystems in the Northern Neotropics. Species are ordered alphabetically within orders and families. Species codes in bold (cladocerans= 32; copepods= 3; ostracodes=17) were included in multivariate analysis. Code indicates the species abbreviations used in figures 6 and 8. For the ecosystem studies see tables 1a,b

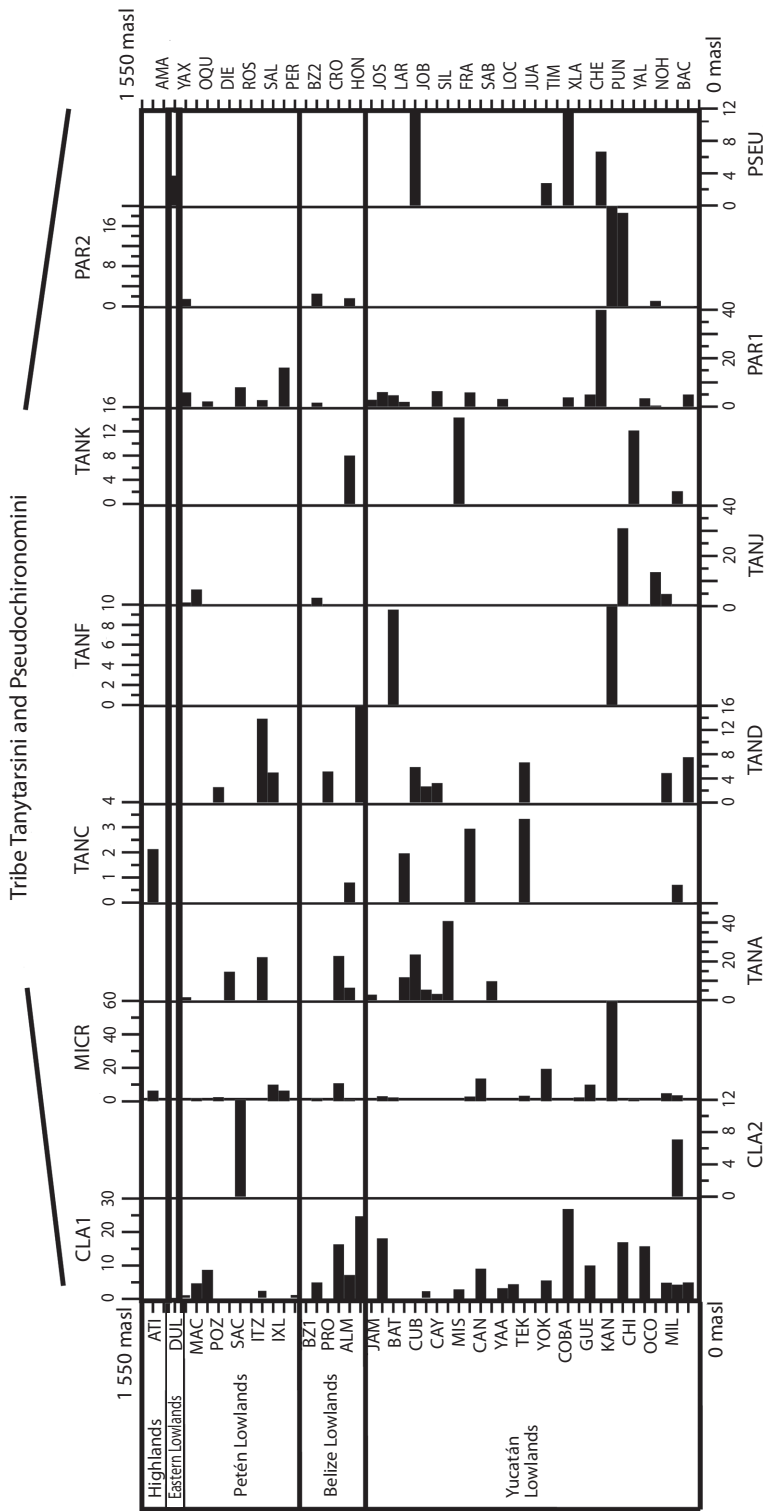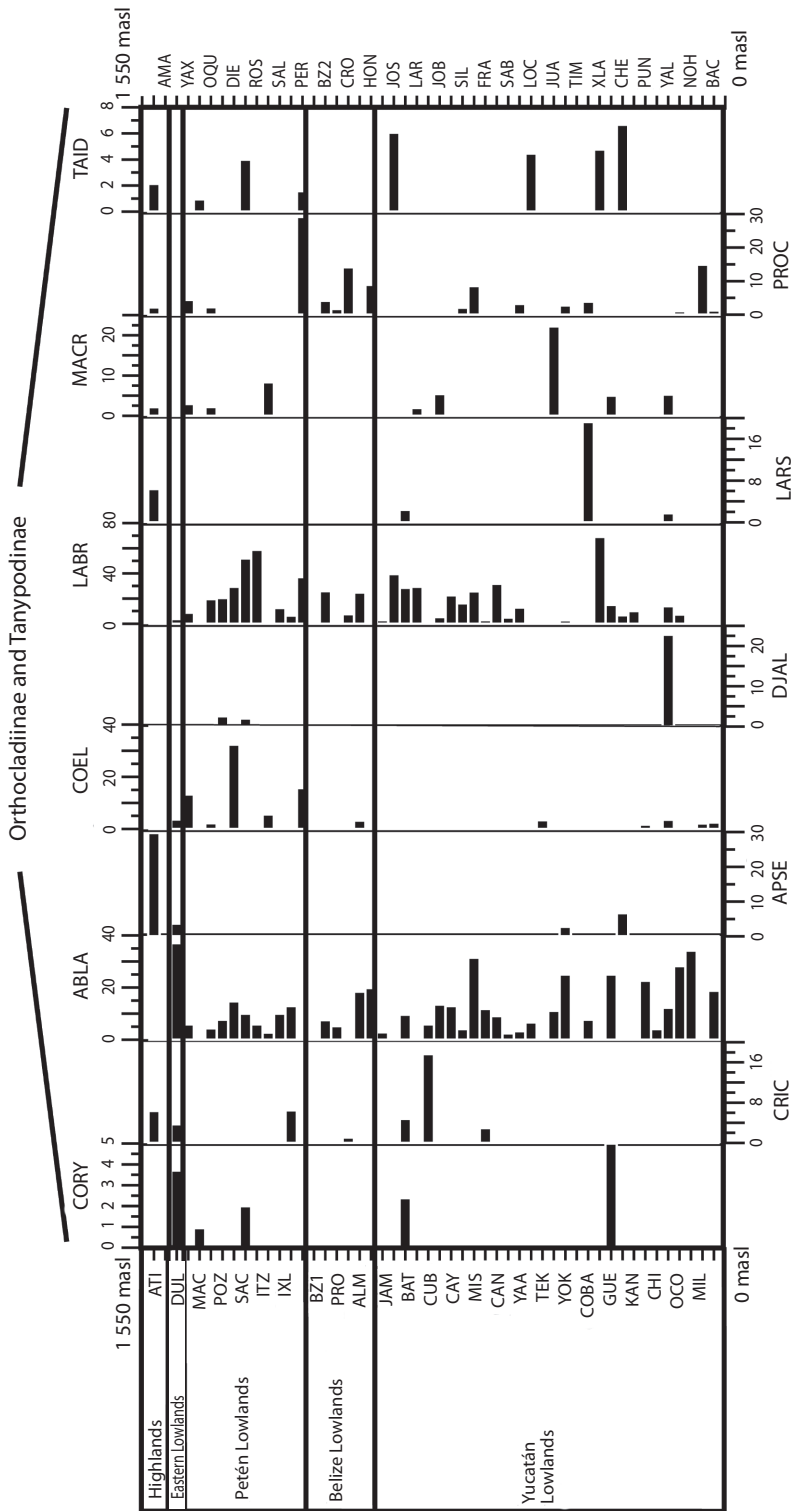| Taxa	Code	Taxa	Code
Dunhevedia odontoplax Sars 1901	DOD	*Physocypria* cf. *denticulata* (Daday 1905)	PDE
Ephemeroporus barroisi (Richard 1894)	EBA	*Physocypria globula* Furtos 1933	PGL
Ephemeroporus hybridus (Daday 1905)	EHY	*Physocypria xanabanica* (Furtos 1936)	PXA
Ephemeroporus tridentatus (Bergamin 1939)	ETR	*Pseudocandona* sp.	PSE
Euryalona orientalis (Daday 1898)	EOR	*Thalassocypria* sp.	THA
Graptoleberis testudinaria (Fischer 1848)	GTE	**Family Cyprididae**	
Karualona muelleri (Richard 1897)	KMU	*Candonocypris* cf. *serratomarginata* (Furtos 1936)	CSE
Kurzia longirostris Daday 1888	KLO	*Chlamydotheca colombiensis* Roessler 1985	CCO
Kurzia polyspina Hudec 2000	KPO	*Cypretta* cf. *brevisaepta* Furtos 1934	CBR
Leberis davidi (Richard 1895)	LDA	*Cypridopsis okeechobei* Furtos 1936	COK
Leydigia striata Birabén 1939	LST	*Cypridopsis vidua* (Müller 1776)	CVI
Notoalona globulosa (Daday 1898)	NGL	*Eucypris* sp.	EUC
Oxyurella ciliata Bergamin 1939	OCI	*Heterocypris punctata* Keyser 1975	HPU
Oxyuella longicaudis Birge 1910	OLO	*Potamocypris* sp.	POT
Pleuroxus quasidenticulatus Smirnov 1996	PQU	*Stenocypris major* (Baird 1859)	SMA
Pseudochydorus globosus (Baird 1843)	PSG	*Strandesia intrepida* Furtos 1936	SIN
Copepods (n=6)		*Trajancypris* sp.	TRA
Class Maxillopoda		**Family Cytheridae**	
Subclass Copepoda		*Perissocytheridea cribosa* (Klie 1933)	PCR
Order Calanoida		**Family Cytherideidae**	
Family Diaptomidae		*Cyprideis* sp.	CIS
Arctodiaptomus dorsalis (Marsh 1907)	ADO	**Family Cytheromatidae**	
Leptodiaptomus siciloides (Lilljeborg 1889)	LSI	*Paracytheroma stephensoni* Puri 1954	PST
Mastigodiaptomus nesus Bowman 1986	MNE	**Family Cytheruridae**	
Mastigodiaptomus reidae Suárez-Morales & Elías- Gutiérrez 2000	MRE	*Cytherura sandbergi* Morales 1966	CSA
		Family Ilyocyprididae	
Prionodiaptomus colombiensis (Thiébaud 1912)	PCO	*Ilyocypris* cf. *gibba* Ramdohr 1808	IGI
Family Pseudodiaptomidae		**Family Limnocytheridae**	
Pseudodiaptomus marshi Wright 1936	PMA	*Cytheridella ilosvayi* Daday 1905	CIL
Ostracodes (n=29)*		*Elpidium bromeliarum* Müller 1880	EBR
Class Ostracoda		*Limnocythere floridensis* Keyser 1976	LFL
Order Podocopida		*Limnocythere opesta* Brehm 1939	LOP
Family Darwinulidae		*Limnocythere* sp.	LIM
Darwinula stevensoni (Brady & Robertson 1870)	DST	**Family Loxoconchidae**	
Family Candonidae		*Loxoconcha* sp.	LOX
Candona sp.	CAN		

* Pérez *et al.* (2011a).

Fig. 2. Plate of selected aquatic bioindicator species. Chironomids: 1. *Beardius* sp., 2. *Cladopelma* sp., 3. *Coelotanypus/Clinotanypus*, 4. *Dicrotendipes* sp., 5. *Goeldochironomus*, 6. *Labrundina* sp., 7. *Parachironomus*, 8. *Stempellina* sp.; Cladocerans: 9. *Anthalona brandorffi* ♀, 10. Postabdomen of *A. brandorffi* ♀, 11. *Coronatella circumfimbriata* ♀, 12. Postabdomen of *C. circumfimbriata* ♀, 13. *C. circumfimbriata* ♂, 14. Postabdomen of *C. circumfimbriata* ♂; Diatoms: 15. *Amphora securicula*, 16. *Brachysira procera*, 17. *Denticula kuetzingii*, 18. *Nitzchia amphibia*, 19. *N. amphibioides*, 20. *Navicula palestinae*; Ostracodes: 21. *Cypridopsis okeechobei*, 22. *Cytheridella ilosvayi*, 23. *Darwinula stevensoni*, 24. *Perissocytheridea cribosa*, 25. *Pseudocandona* sp., 26. *Stenocypris major*, 27. *Thalassocypria* sp.

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Fig. 3a. Relative abundances (%) of chironomid (morpho)species (Chironomini) of the northern Neotropics training set along an altitude gradient. (Morpho)species are presented in alphabetical order and full species names are in table 2.

Fig. 3b. Relative abundances (%) of chironomid (morpho)species (Tanytarsini and Pseudochironomini) of the northern Neotropics training set along an altitude gradient. (Morpho) species are presented in alphabetical order and full species names are in table 2.

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Fig. 3c. Relative abundances (%) of chironomid (morpho)species (Orthocladiinae and Tanypodinae) of the northern Neotropics training set along an altitude gradient. (Morpho) species are presented in alphabetical order and full species names are in table 2.

in the Belizean lowlands. Species typical of the Yucatán lowlands were *Cladotanytarsus* sp. 1, *Goeldochironomus* sp. and *Polypedilum* sp.1 and sp. 2.

Diatoms: Diatoms were the most abundant and diverse taxonomic group studied. Figures 4 a, b show the most abundant diatom species (>2 waterbodies). Pennate diatoms displayed the highest number of families and species. In contrast, centric diatoms were only represented by four families (Tables 3 a-e). Naviculaceae represents 162 of the 282 diatom species and were mainly distributed in lowland waterbodies on the Yucatán Peninsula. Widely distributed diatom species, i.e. those found in >20 waterbodies, include *Brachysira procera*, *Cyclotella meneghiniana, Denticula kuetzingii, Encyonema densistriata*, *Mastogloia smithii* and *Nitzschia amphibia*. *Nitzschia amphibia* and *Ulnaria delicatissima* var. *angustissima* were found in all highland lakes. *Aulacoseira granulata*, *Fragilaria crotonensis*, *Ulnaria acus* and *Ulnaria ulna* were present in three of four sampled highland lakes. The dominant species in hypereutrophic Lake Amatitlán were *Cyclotella meneghiniana* and *Discostella* aff. *pseudostelligera. Fragilaria crotonensis* is a species restricted to the highlands and the Eastern lowlands in Guatemala, whereas *Staurosirella pinnata* was only collected in Lake Izabal, in the Eastern lowlands of Guatemala. Interestingly, few waterbodies have a predominantly monospecific diatom flora, e.g. Lake Rosario (93.6% *Nitzschia amphibioides*), Lake Atitlán (86.2% *Fragilaria crotonensis*)*,* Almond Hill Lagoon 81.2% *N. amphibia*) and the pond called Belize 2 (72.6% *Encyonema densistriata*).

Microcrustaceans: Cladocera were the most diverse group of microcrustacea, with 51 species belonging to seven families. Ostracodes were next, with 29 species distributed in 10 families. Calanoid copepods followed, with six species belonging to two families (Tables 4 a, b). Figures 5 a, b and figure 6 show the relative a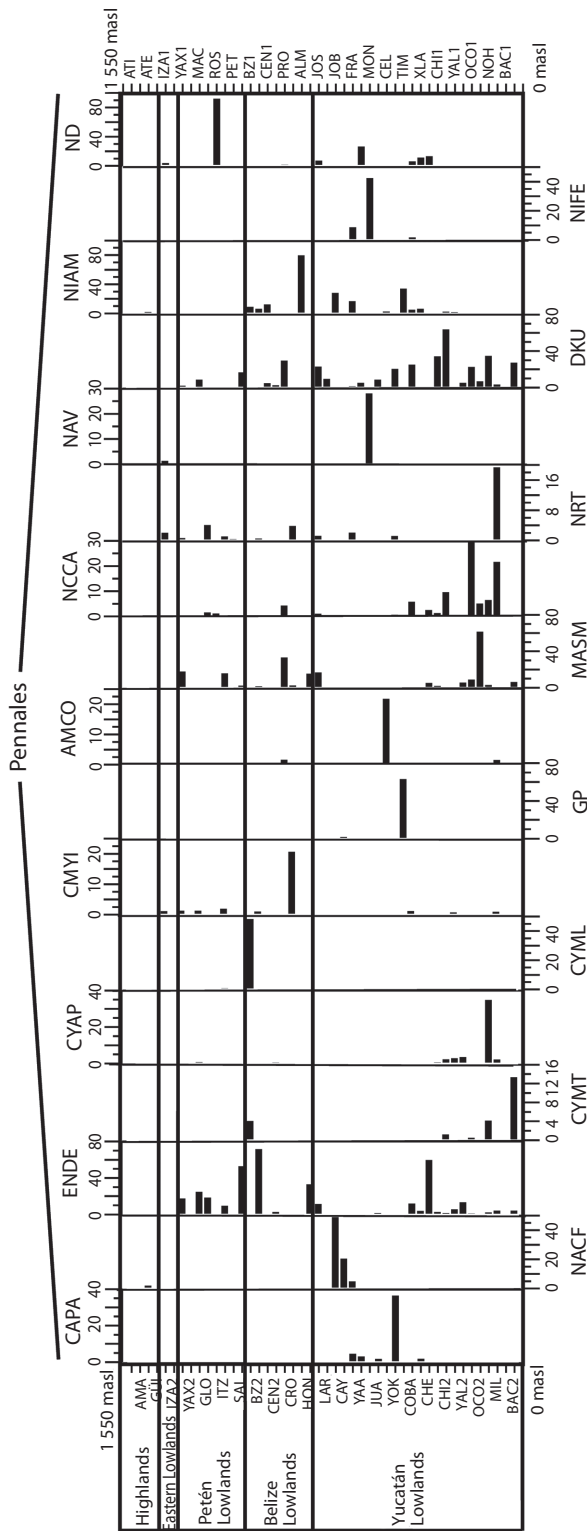bundances of the most widespread cladoceran, copepod and ostracode species, i.e. those present in >2 aquatic environments.

Cladocerans: Most collected cladoceran species belong to the order Anomopoda, family Chydoridae (Table 4 a). The greatest numbers of species were collected in lakes, ponds, and coastal waterbodies, whereas few species were collected in "cenotes" and rivers, where shells without soft parts were generally found. Assemblages in the highlands were dominated by *Bosmina huaronensis*, *Ceriodaphnia dubia*, *Daphnia mendotae*, *Daphnia pulicaria*, *Moinodaphnia minuta* and *Simocephalus congener*. *Daphnia pulicaria* and *Simocephalus congener* are restricted to highland lakes. *Daphnia mendotae* was the only species collected in highly productive Lake Amatitlán. *Ceriodaphnia* cf. *rigaudi* and *Bosmina huaronensis* displayed high relative abundance (>35%) in the Eastern lowlands of Guatemala. *Dunhevedia odontoplax* was the only species restricted to the Petén and Belize lowlands, and like *Ceriodaphnia dubia,* was absent in the Yucatán lowlands. The greatest numbers of cladoceran species were collected in the Mexican lowlands (n=41), followed by the Belizean lowlands (n=36), and the Guatemalan lowlands (n=25). Cladoceran communities in the lowlands were dominated by *Diaphanosoma brevireme*, *Simocephalus serrulatus*, *Bosmina tubicen*, *Ilyocryptus spinifer*, *Macrothrix elegans*, *Macrothrix* cf. *spinosa*, *Anthalona verrucosa*, *Chydorus brevilabris* and *Chydorus eurynotus*. Rare cladoceran species collected in only one waterbody of the lowlands include *Coronatella circumfimbriata* (Loché), *Dadaya macrops* (Jamolún), *Karualona karua* (Cenote), *Kurzia longirostris* (Chacan-Bata) and *Oxyurella ciliata* (Cayucón).
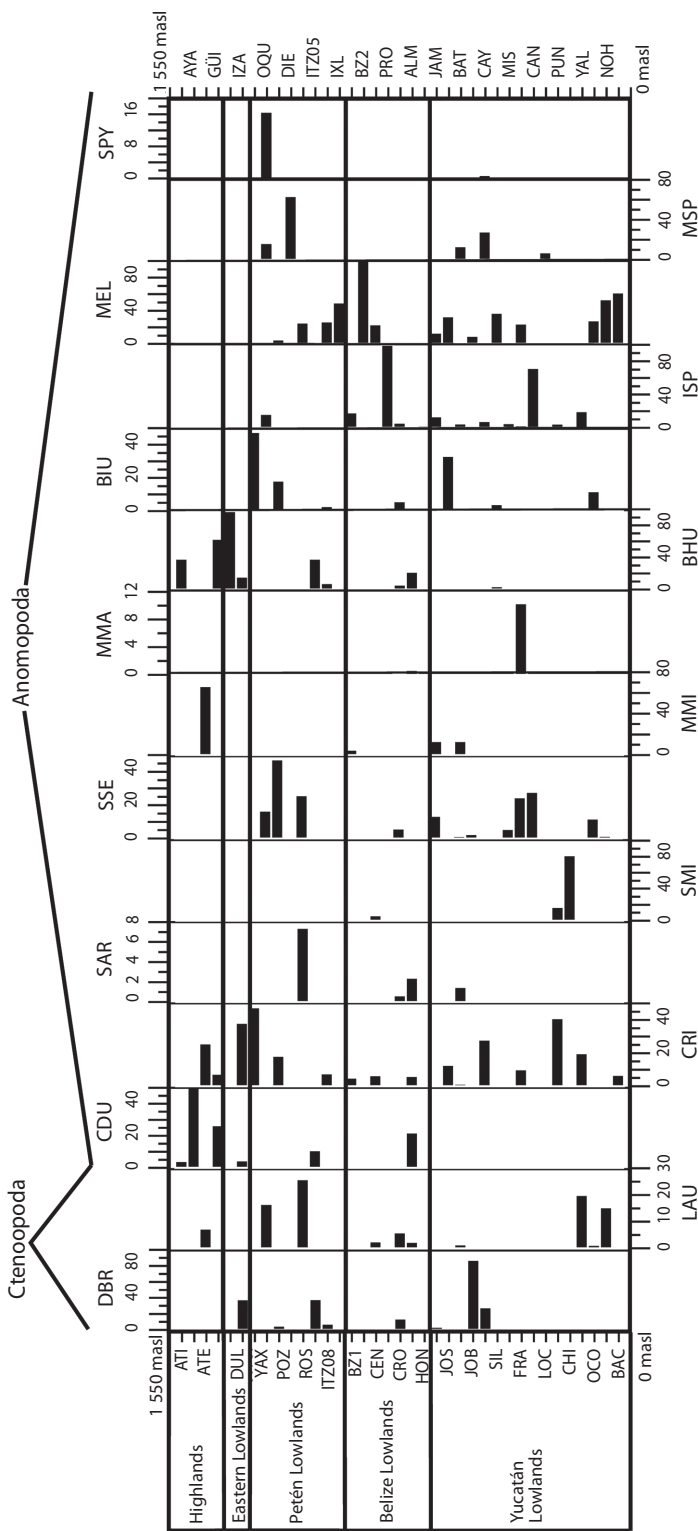
Copepods: Only calanoid copepods were studied, and only six species belonging to the families Diaptomidae and Pseudodiaptomidae were identified (Table 4 b, Fig. 6). Copepod species found in highland lakes include *Arctodiaptomus dorsalis*, *Leptodiaptomus siciloides* and *Prionodiaptomus colombiensis*.

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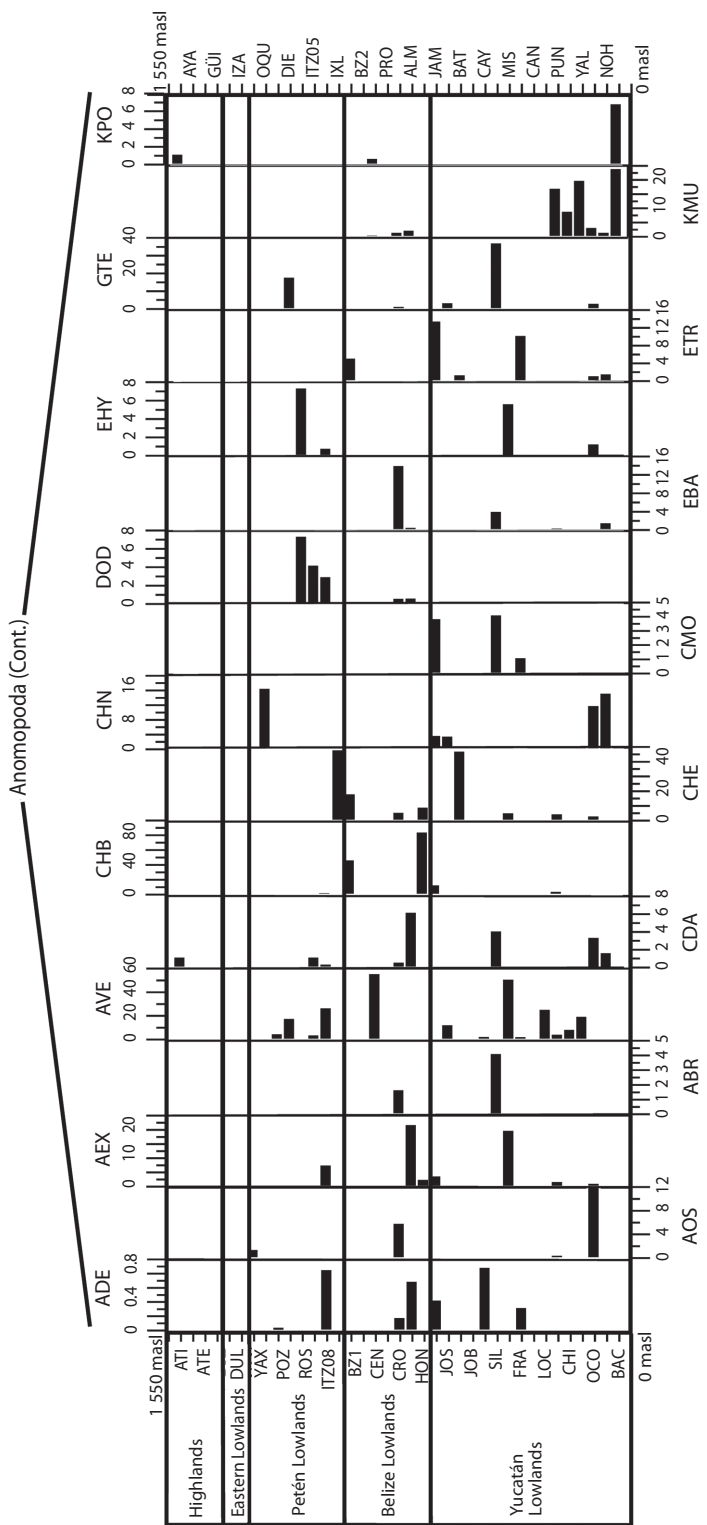
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Fig. 4a. Relative abundances (%) of diatom species (Centrales and Pennales) of the northern Neotropics training set along an altitude gradient. Species are presented in alphabetical order and full species names are in table 3.
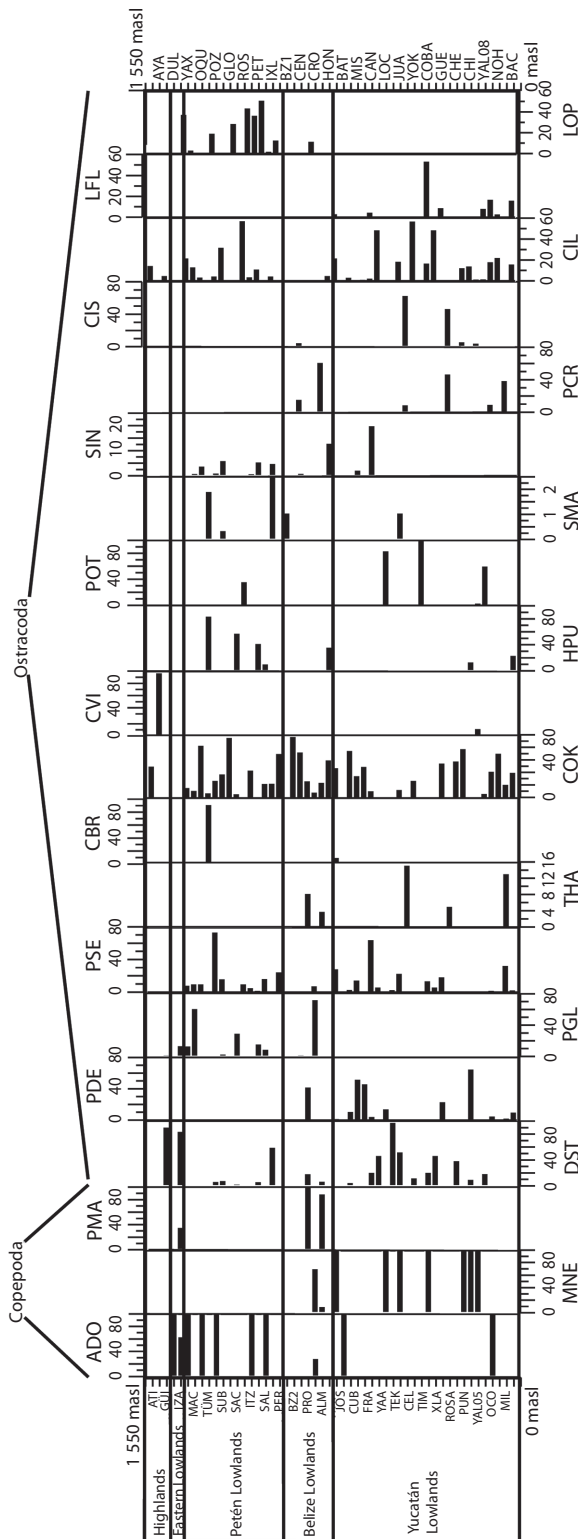
Fig. 4b. Relative abundances (%) of diatom species (Pennales, cont.) of the northern Neotropics training set along an altitude gradient. Species are presented in alphabetical order and full species names are in table 3.

Fig. 5a. Relative abundances (%) of cladoceran species (Ctenopoda and Anomopoda) for the northern Neotropics training set along an altitude gradient. Species are presented in alphabetical order and full species names are in table 4.

Fig. 5b. Relative abundances (%) of cladoceran species (Anomopoda, cont.) for the northern Neotropics training set along an altitude gradient. Species are presented in alphabetical order and full species names are presented in table 4.

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Fig. 6. Relative abundances (%) of ostracode and copepod species for the northern Neotropics training set along an altitude gradient. Species are presented in alphabetical order and full species names are in table 4.
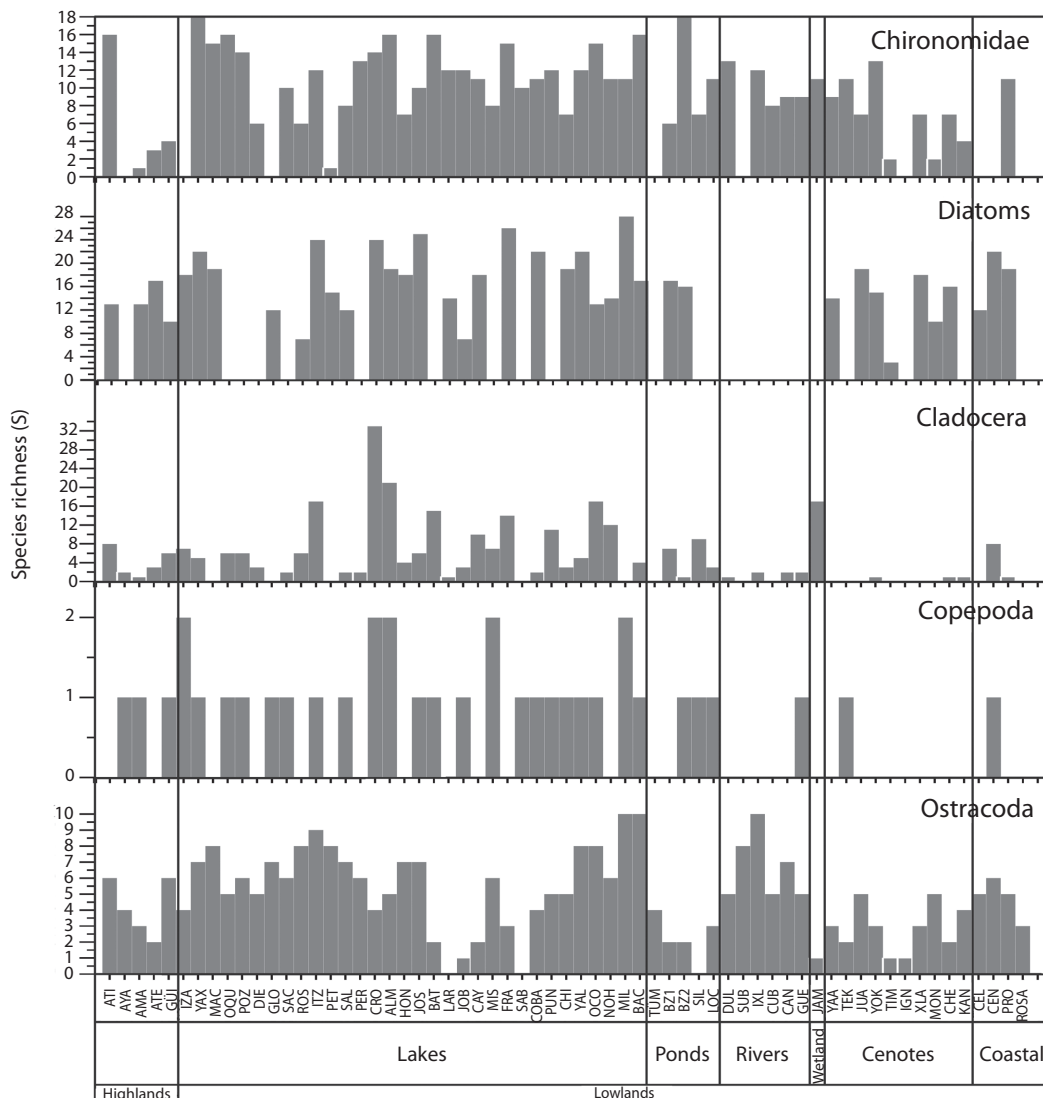
Arctodiaptomus dorsalis was the only species collected in hypereutrophic Lake Amatitlán. *Leptodiaptomus siciloides* and *P. colombiensis* are rare species that live in the highlands and were collected in the oligotrophic Laguna de Ayarza and in Lake Güija. *Arctodiaptomus dorsalis* was widely distributed in the lowlands, but mostly dominated aquatic ecosystems in the Petén lowlands. *Mastigodiaptomus nesus* is restricted to the Belize and Yucatán lowlands, whereas *Pseudodiaptomus marshi* inhabits the Petén and Belize lowlands. Except for *Mastigodiaptomus nesus,* which was found in Cenote Juarez, no calanoid copepods were collected from "cenotes" and rivers.

Ostracodes: Partial results on ostracode distribution in the Yucatán Peninsula and surrounding areas were published by Pérez *et al.* (2011b) and therefore only the most important results are presented here. Ostracoda was the group of microcrustaceans that displayed the highest number of families (Table 4 b, Fig. 6). Families with highest numbers of species included Cyprididae (n=11), Candonidae (n=6) and Limnocytheridae (n=5). The genera *Limnocythere* and *Physocypria* had the highest numbers of species (n=3). Ubiquitous species include *Cypridopsis okeechobei*, *Cytheridella ilosvayi*, *Darwinula stevensoni* and *Pseudocandona* sp. (Fig. 6). There is a clear difference between highland and lowland assemblages and between fresh and brackish water assemblages. Species typical of the highlands are *Candona* sp., *Chlamydotheca colombiensis*, *Ilyocypris* cf. *gibba*, *Limnocythere* sp. and *Trajancypris* sp. *Physocypria denticulata* inhabits aquatic ecosystems of the lowlands in Belize and Yucatán, whereas *Physocypria globula* is restricted to the Petén lowlands. Lowland rare species *Cytherura sandbergi*, *Elpidium bromeliarum*, *Eucypris* sp., and *Physocypria xanabanica*, were collected in Celestún, Río Dulce, Laguna Rosario, and in the small pond Belize 1, respectively. *Cypretta brevisaepta* was abundant in Lake Oquevix and in a small pond nearby.

Species richness and diversity in aquatic ecosystems: The species richness (S) and the Shannon Wiener diversity index (H) of diatoms, chironomids and microcrustaceans for the 63 studied aquatic ecosystems are shown in figures 7 a, b. Ostracodes were collected in 59 waterbodies, chironomids in 53 and cladocerans in 46. Copepods were found in only 30 aquatic environments. Lowland waterbodies (<450m.a.s.l.) displayed highest diversity values, up to H=2.6 (diatoms), and greatest species richness, as many as 33 species (cladocerans). Lowland waterbodies Crooked Tree Lagoon, Lake Petén Itzá and Almond Hill Lagoon, followed by Lakes Yaxhá, Macanché, San José Aguilar, Cayucón, San Francisco Mateos, Cobá, Yalahau, Ocom, Nohbec, Milagros and Bacalar, yielded the highest overall species richness (up to S=77) on the Yucatán Peninsula and in surrounding areas.

Chironomids and ostracodes were present in all waterbody types (Fig. 7 a). Sampled rivers lacked diatoms and cladocerans. Copepods were scarce in rivers, "cenotes" and coastal waterbodies. The Jamolún wetland was dominated by chironomids and cladocerans. Cladocerans and ostracodes were present in all the highland lakes. Lakes Amatitlán, Gloria, Petexbatún, Celestún and Laguna Rosada displayed H values of 0 for chironomids, cladocerans and calanoid copepods. Ostracodes yielded H values >0, in TÜM, a pond near Lake Oquevix, in the Subín river and in Laguna Rosada. Cenote San Ignacio Chocholá displayed an H=0 for all bioindicators. Sabanita yielded an H>0 only for chironomids (H=1.8).

Chironomids were prominent mainly in lowland lakes. Up to 18 morphospecies were collected in Lake Yaxhá and in the pond Belize 2, and 16 species were collected in Lakes Oquevix, Almond Hill Lagoon, Chacan-Bata, Bacalar and highland Guatemala Lake Atitlán (Fig. 7 a). Hypereutrophic Lake Amatitlán had a monospecific chironomid assemblage of *Chironomus anthracinus*. *Dicrotendipes* sp. was the only species collected in Lake Petexbatún, southern Petén. Highest diversity was reported in Lakes Oquevix (H=2.50) and Yaxhá

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Fig. 7a. Species richness (S) of the five studied taxonomic groups (chironomids, diatoms, cladocerans, copepods and ostracodes) in aquatic ecosystems of the northern Neotropics.

(H=2.54). Relatively low diversities (H≤0.7) were determined in Cenotes Petén de Monos and Timul, Northern Yucatán Peninsula.

Diatoms were generally more diverse than other bioindicators in each waterbody. The number of diatom species per lake, if present, ranged from 7 to 28. Highest numbers of species (S>20) were reported in Lakes Petén Itzá, Yaxhá, Cobá, Yalahau, Milagros, San

José Aguilar, San Francisco Mateos, Cenote and Crooked Tree Lagoon. Among sampled ponds, only Belize 1 and 2 possessed diatoms. In oligotrophic Crater Lake Ayarza, no diatoms were found. High diatom diversities (H≥2.0) were determined in Lakes Yaxhá, Macanché, Petén Itzá, San José Aguilar, San Francisco Mateos, Cobá, Yalahau, Milagros, Bacalar, Crooked Tree Lagoon, Cenote Xlacah and

Fig. 7b. Shannon Wiener diversity index (H) of the five taxonomic groups (chironomids, diatoms, cladocerans, copepods and ostracodes) in aquatic ecosystems of the northern Neotropics.

in coastal waterbody Celestún. In contrast, Lakes Atitlán, Rosario, Almond Hill Lagoon and Cenote Timul were characterized by low diversities (H<1.0).

Highest cladoceran species richness was found in Crooked Tree Lagoon (33),

Almond Hill Lagoon (21), Lakes Petén Itzá and Ocom, and in the Jamolún wetland (17). Few cladocerans were found in "cenotes" and coastal environments. The highest diversity index (H=2.4) was also found in Crooked Tree Lagoon. Male specimens were rare and

reported for the cladoceran species *Ceriodaphnia* cf. *rigauda*, *Diaphanosoma brevireme*, *Ephemeroporus barroisi*, *Macrothrix elegans* and *Macrothrix paulensis*.

Highest numbers of ostracode species (≤10) were collected in Lakes Bacalar and Milagros in Eastern Yucatán and in Ixlú River, Northern Guatemala (Fig. 7 a). The largest and deepest lake, Petén Itzá, possessed nine ostracode species. Only a few waterbodies on the Yucatán Peninsula lacked ostracodes: Chacan Lara, Sabanita and Silvituc. Ostracodes were abundant on the Yucatán Peninsula, especially in the lowlands of Petén (S≥5). Rivers were characterized by relatively high numbers of species (S=5-10). Ostracodes in "cenotes" and in the Jamolún wetland were not as abundant as in other aquatic ecosystems. Ostracodes were highly diverse in rivers, and lowland lakes (H≤1.8). Ponds displayed low diversities (H≤0.5) except for a pond near Lake Oquevix (TÜM, H=1.0). Brackish waterbodies were characterized by diversity indices ≤1.29.
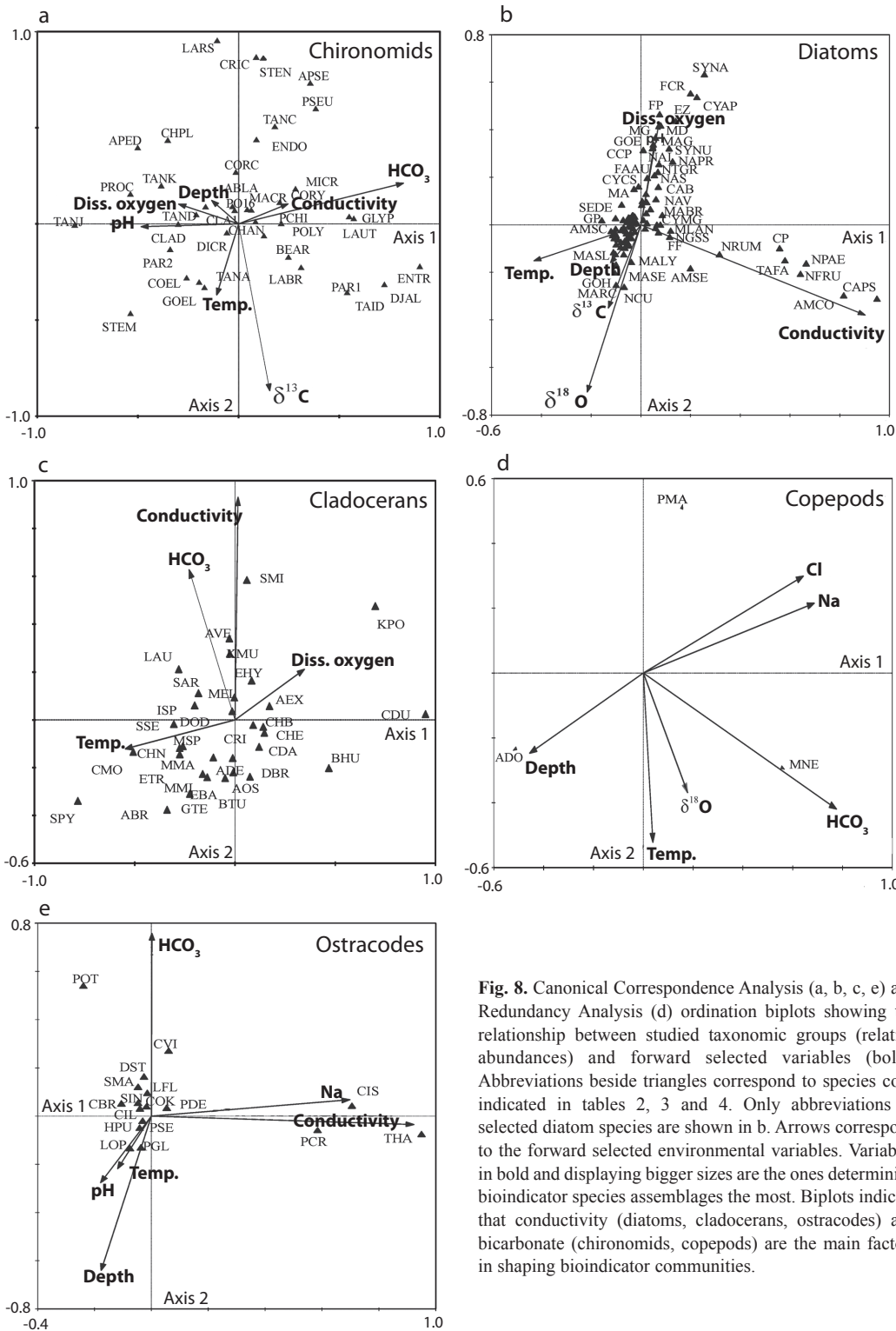
Copepods were less abundant and diverse than chironomids, diatoms, cladocerans and ostracodes. Few calanoid copepod species (S≤2) were collected and were rarely found in rivers, "cenotes" or coastal waterbodies. Copepod diversity in the study area was ≤0.69. Highest diversities were reported in Lakes Bacalar and San Francisco Mateos, followed by Lakes Izabal (H=0.65), Crooked Tree Lagoon (H=0.60) and Almond Hill Lagoon (H=0.33).

Calibration of bioindicators on the Yucatán Peninsula: We assessed relationships between the various studied biological groups and environmental variables. Quantitative relations between chironomids, diatoms, cladocerans and ostracodes and environmental variables were assessed using a unimodal model with 14 explanatory variables, because gradient lengths were ≥3 standard deviations (SDs). The first two axes in the DCA explained 17.7% of chironomid variability, 16.3% of diatom variability, 21.5% of cladoceran variability, and 27.8% of the ostracode species data. The sum of eigenvalues was 2.8 for chironomids,

4.3 for cladocerans, 6.1 for diatoms and 3.1 for ostracodes.

To improve the performance of the CCA model, the number of environmental variables was reduced to include only those that best explain the bioindicator distributions. Forward-selected variables displayed low inflation factors (<5). Seven variables were related to chironomid (HCO_3, $\delta^{13}C$, pH, temperature, conductivity, dissolved oxygen, water depth) and diatom relative abundances (conductivity, $\delta^{18}O$, dissolved oxygen, temperature, pH, $\delta^{13}C$, water depth), four to cladoceran (conductivity, HCO_3, temperature, dissolved oxygen) and six to ostracode abundances (conductivity, HCO_3, Na, water depth, temperature, pH) (Fig. 8). For copepods, a linear model was chosen because the gradient length was only 2.15 SD units. The first two axes in the DCA explained 72.9% of the variability in the copepod species data. The sum of eigenvalues was 1.6. Six forward-selected variables (HCO_3, Cl, Na, temperature, water depth, $\delta^{18}O$) were included in the final RDA. In the final CCAs and RDA, HCO_3 was the main factor controlling chironomid and copepod assemblages on the Yucatán Peninsula (Fig. 8). Diatom, cladoceran and ostracode communities are more influenced by conductivity. $\delta^{13}C_{DIC}$, a lake productivity proxy, and lakewater $\delta^{18}O$, a proxy for changes in the balance between evaporation and precipitation and perhaps conductivity, were the second most important factors affecting chironomid and diatom distributions, respectively (Fig. 8). The final CCA for chironomids explained 4.8% ($\lambda1=0.14$, $\lambda2=0.11$), 6.8% for diatoms ($\lambda1=0.42$, $\lambda2=0.33$), 6.4% for cladocerans ($\lambda1=0.27$, $\lambda2=0.15$), 9.9% for ostracodes ($\lambda1=0.31$, $\lambda2=0.13$) of the variability in species data, and the final RDA for copepods explained 24.9% ($\lambda1=0.25$, $\lambda2=0.11$) of the variability in species data (Table 5).

Chironomid species such as *Stempellina* sp., *Goeldochironomus* sp., *Coelotanypus*/*Clinotanypus*, *Paratanytarsus* sp. 2, Tanytarsini A and Tanytarsini J were positioned in the lower left quadrant of the CCA ordination biplot (Fig. 8 a). These species are typical of lowland waterbodies, especially those located on the

Fig. 8. Canonical Correspondence Analysis (a, b, c, e) and Redundancy Analysis (d) ordination biplots showing the relationship between studied taxonomic groups (relative abundances) and forward selected variables (bold). Abbreviations beside triangles correspond to species code indicated in tables 2, 3 and 4. Only abbreviations of selected diatom species are shown in b. Arrows correspond to the forward selected environmental variables. Variables in bold and displaying bigger sizes are the ones determining bioindicator species assemblages the most. Biplots indicate that conductivity (diatoms, cladocerans, ostracodes) and bicarbonate (chironomids, copepods) are the main factors in shaping bioindicator communities.

Results of the Canonical Correspondence Analysis (CCA) and Redundancy Analysis (RDA) using chironomid,
diatom, cladoceran, ostracode and copepod species data and forward selected variables (FSV)

	CCA				
Axes	1	2	3	4	Total inertia
Chironomids; FSV=7					
Eigenvalues	0.141	0.110	0.087	0.080	2.909
Species-environment correlations	0.792	0.781	0.864	0.738	
Cumulative percentage variance					
of species data	4.8	8.6	11.6	14.4	
of species-environment relation	24.8	44.3	59.6	73.6	
Sum of all canonical eigenvalues					0.567
Diatoms; FSV=7					
Eigenvalues	0.416	0.329	0.260	0.184	6.111
Species-environment correlations	0.890	0.947	0.834	0.831	
Cumulative percentage variance					
of species data	6.8	12.2	16.4	19.4	
of species-environment relation	26.9	48.2	65.0	76.9	
Sum of all canonical eigenvalues					1.545
Cladocerans, FSV=4					
Eigenvalues	0.273	0.147	0.085	0.069	4.247
Species-environment correlations	0.771	0.677	0.635	0.611	
Cumulative percentage variance					
of species data	6.4	9.9	11.9	13.5	
of species-environment relation	47.5	73.1	87.9	100.0	
Sum of all canonical eigenvalues					0.574
Ostracodes; FSV=6					
Eigenvalues	0.312	0.133	0.103	0.047	3.140
Species-environment correlations	0.792	0.611	0.561	0.398	
Cumulative percentage variance					
of species data	9.9	14.2	17.4	18.9	
of species-environment relation	49.7	70.9	87.3	94.8	
Sum of all canonical eigenvalues					0.627
	RDA				
Calanoid copepodes, FSV=4					
Eigenvalues	0.249	0.106	0.039	0.382	1.000
Species-environment correlations	0.637	0.670	0.510	0.000	
Cumulative percentage variance					
of species data	24.9	35.5	39.4	77.6	
of species-environment relation	63.1	90.1	100.00	0.0	
Sum of all canonical eigenvalues					0.394

Eastern part of the Yucatán Peninsula, Belize, and the central and Eastern areas of the Petén Lake District. Species located in the upper left quadrant inhabit mainly lowland aquatic ecosystems, except for *Apedilum* sp. This species was collected at both high and low elevations, but was more abundant in highland Lake Atitlán. *Apsectrotanypus* sp., *Cricotopus* spp., Tanytarsini C and *Stenochironomus* sp. inhabit highland lakes and were positioned in the right upper quadrant of the biplot. The chironomid species *Glyptotendipes* sp. 2 in the upper part of the right quadrant of the biplot was mainly collected in "cenotes," Lake Oquevix, Río

Dulce and Loché pond. *Chironomus anthracinus*, located in the lower right quadrant, was the only species present in hypereutrophic Lake Amatitlán. *Labrundina* sp., *Beardius* sp. and *Paratanytarsus* sp.1 were widely distributed in the lowlands of the Yucatán Peninsula and surrounding areas.

Diatom species *Halamphora coffeaeformis*, *Campylostylus normannianus*, *Nitzschia frustulum*, *Navicula palestinae*, *Tabularia fasciculata*, *Navicula salinarum*, *Amphora securicula* and *Cocconeis placentula* are located in the lower quadrant of the biplot (Fig. 8 b) and are characteristic of lakes with high conductivities, up to 38.2mS/cm. Species characteristic of lower conductivities and most diatom species typical of fresh waters are located near the central part of the biplot.

The CCA biplot for cladocerans indicates that water conductivity influences species distribution on the Yucatán Peninsula (Fig. 8 c). *Simocephalus mixtus* and *Karualona muelleri* were positioned in the upper right and left quadrant of the CCA biplot, respectively, because they dominated lakes with high conductivities (up to ~6 000μS/cm) such as Cenote, Almond Hill Lagoon, Chichancanab, Punta Laguna, Yalahau, among others. *Kurzia polyspina* was located in the upper right quadrant because it prefers waters with dissolved oxygen concentrations between 7.3 and 8.3mg/L. *Streblocerus pygmaeus*, located in the lower left quadrant of the CCA biplot, is a species typical of warm lake waters (>25°C) with lower conductivities (<350μS/cm) such as Oquevix, Crooked Tree Lagoon and Cayucón. The dominant cladocerans in highland Lakes Atitlán, Amatitlán, Ayarza and Güija were *Ceriodaphnia dubia* and *Bosmina huaronensis*, located in the upper and lower right quadrants, respectively. *Moina minuta* was typical of Lake Atescatempa, Izabal, Chacan-Bata, pond Belize 1 and the Jamolún wetland. *Daphnia mendotae* was the only species identified in surface sediments from Lake Amatitlán.

Similar to the findings for chironomids, bicarbonate determined calanoid copepod distribution in the study area (Fig. 8 d). Few specimens were collected in the highlands of Southern Guatemala, thus all species on the biplot are typical of the lowlands. *Arctodiaptomus dorsalis*, in the lower left quadrant of the ordination diagram, dominated lakes with fresh waters, and was absent in "cenotes" and coastal waterbodies. *Mastigodiaptomus nesus*, in the lower right quadrant, is typical of HCO_3-rich waters (125-710mg/L), such as San José Aguilar, Loché, Juárez, Cobá, Punta Laguna, Chichancanab and Yalahau. *Pseudodiaptomus marshi*, in the upper right quadrant, is typical of lakes at low altitudes (<5m.a.s.l.), such as Lake Izabal, Guatemala and Lagoons Progreso and Almond Hill, Belize. This species was also collected in waterbodies displaying slightly higher conductivities, such as Bacalar and Lagoons Progreso and Almond Hill.

The CCA biplot for ostracodes suggests that conductivity, followed by HCO_3, are the main factors controlling species distribution (Fig. 8 e). *Perissocytheridea cribosa*, *Cyprideis* sp. and *Thalassocypria* sp. are situated in the positive part of axis 1, indicating their preference for high-conductivity waters (750μS/cm-55.3mS/cm). Ostracode species that prefer freshwaters are situated in the center of the CCA biplot. *Cypridopsis vidua*, in the upper right quadrant of the CCA biplot, was more abundant in highland Lake Ayarza, Guatemala. Species tolerating the hypereutrophic water of Lake Amatitlán include *Candona* sp., *Cypridopsis vidua* and *Darwinula stevensoni*. Ostracodes displaying high abundances in highland and lowland lakes included *Cypridopsis okeechobei*, *Cytheridella ilosvayi* and *Darwinula stevensoni*. *Potamocypris* sp., in the upper left quadrant, was collected in Lakes Rosario, Yalahau, Loché pond and Cenote Timul, suggesting its preference for warm waters (up to 32°C) and waters with HCO_3 concentrations as high as 707mg/L.

DISCUSSION

Neotropical aquatic bioindicators across broad trophic and climatic gradients: We have provided a first comprehensive list of

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modern diatom (282) and chironomid (66) species for the region, along with species distributions, relative abundances in each lake, and quantitative ecological information. CCA ordination biplots, relating bioindicator species and forward selected variables, distinguish between taxa typical of highland vs. lowland lakes, brackish vs. fresh waters, alkaline vs. acidic waters, and lakes of different trophic states. Most bioindicator species live at low elevations (<450m.a.s.l.), with fewer species and individuals in highland lakes. In general, diatom, cladoceran and ostracode communities are most affected by conductivity, reflecting lake water chemical composition, marine influence (Perry *et al.* 1995) and the N-S precipitation gradient in the Yucatán Peninsula. Species of these taxonomic groups presented characteristic faunas of fresh and brackish waters. Bicarbonate controls chironomid and copepod distribution in the study area. Concentration of bicarbonate in lake waters is an important variable in the study area because most of the studied lakes lie in karst terrain. Another related factor could be the greater abundance of edible algae in hard water lakes (Ghadouani *et al.* 1998). The second determinant variable for chironomid distribution was $\delta^{13}C_{DIC}$, an indicator of lake water productivity (McKenzie 1985), indicating the potential of some chironomid species as indicators of lake trophic state. Our results demonstrate that aquatic bioindicators on the Yucatán Peninsula are highly sensitive to changes in water column conductivity, alkalinity and trophic state.

Sánchez *et al.* (2002) identified 75 diatom species in "cenotes" and anchialine caves on the Eastern Yucatán Peninsula. Similar to our findings, they reported that pennate diatoms were the dominant group. Few diatoms were of marine origin. Similar results were also found in aquatic ecosystems of Costa Rica (Haberyan *et al.* 1997), El Salvador (Rivas Flores *et al.* 2010) and Nicaragua (Swain 1966). All studies indicated that Naviculaceae is a dominant family in waterbodies of the Northern Neotropics. Six species belonging to Naviculaceae, Thalassiosiraceae and Bacillariaceae

were hydrochemically tolerant and displayed wide distributions: *Brachysira procera*, *Encyonema densistriata*, *Mastogloia smithii*, *Denticula kuetzingii*, *Cyclotella meneghiniana* and *Nitzschia amphibia*. *Nitzschia amphibia* tolerates broad trophic state and conductivity ranges. *Cyclotella meneghiniana* and *Discostella* aff. *pseudostelligera* dominated the hypereutrophic waters of Lake Amatitlán, Guatemala. Velez *et al.* (2011) used diatoms and other variables to infer environmental and cultural changes in and around this highland lake. They suggested that *C. meneghiniana* is an indicator of low lake levels, whereas *N. amphibia* indicates eutrophic waters. Highland and lowland lakes differ in their bioindicator communities, as some species are highly sensitive and restricted to specific areas. *Fragilaria crotonensis* is a species typical of the highlands and Eastern lowlands in Guatemala. *Fragilaria* species indicate oligotrophic to mesotrophic conditions (Castellanos & Dix 2009). This species dominated (86.2%) in Lake Atitlán, a lake that experienced extensive cyanobacteria (*Lyngbya hieronymusii*/*birgei*/*robusta*) blooms in October 2009 (Rejmánková *et al.* 2011). When we visited Lake Atitlán in March 2008, the lake still displayed oligo- to mesotrophic conditions, indicated by the dominance of *F. crotonensis*, shortly before the first cyanobacteria bloom, which occurred in December 2008.

Vinogradova & Riss (2007) reported 84 chironomid taxa, mainly morphospecies, from 18 lakes on the Yucatán Peninsula. In their study, the dominant chironomid species were *Cladopelma lateralis* and species belonging to the genus *Tanytarsus*. Our dataset included a larger number of aquatic ecosystems (n=63), however results from both studies are similar. Few chironomid taxa are restricted to specific areas. Rather, the dipterans seem to tolerate a broad range of environmental conditions. *Chironomus anthracinus* displayed high relative abundance in most sampled waterbodies and the larvae have been to shown to be among the dominant food items of fish (Armitage *et al.* 1995). This species was very abundant in many of our surface sediment samples. It

tolerates eutrophic waters (Porinchu & Mac-Donald 2003), which characterize many lowland and some highland lakes in the study area. For instance, *C. anthracinus* was the only dipteran species collected in hypereutrophic Lake Amatitlán, Guatemala. For decades, this highly productive lake has received wastewater, delivered by its main inflow river, the Río Villalobos. This species was also collected in Cenote Timul, which displayed high $\delta^{13}C_{DIC}$ values of +13.6‰ (Pérez *et al.* 2011a). These results illustrate that *C. anthracinus* can be used as an indicator of highly productive waters in the Northern Neotropics. A larger number of species (n=51) inhabit the lowlands. Fewer species were identified in the highlands (n=15), suggesting that chironomids are very abundant in low-elevation neotropical regions, similar to findings in Africa (Eggermont *et al.* 2010), where 81 chironomid taxa were collected across an altitude gradient (489-4 575m.a.s.l.) and in Brazil (de Oliveira Roque & Trivinho-Strixino 2007), where 191 morphospecies were collected.

Cladocerans dominated the microcrustacean communities in the study area. Fifty-one species were collected in the waterbodies and the greatest number of species belonged to the family Chydoridae. Many species of Chydoridae have great value as water-quality indicators because they are highly sensitive to changes in lake trophic state (de Eyto *et al.* 2002). Cladocerans and copepods are the two taxonomic groups most studied on the Yucatán Peninsula and in surrounding areas (Elías-Gutiérrez *et al.* 2008). Mexico has been actively involved in studying the systematics of Cladocera (Elías-Gutiérrez *et al.* 2006). Therefore, identification of collected cladocerans and copepods to species level was possible. Elías-Gutiérrez (2006) reported a total of 162 cladoceran species for two regions of Mexico (Morelos and southeast Mexico), four being endemic species of Southeast Mexico. Some of the cladoceran species we collected are widely distributed in the Northern Neotropics and South America. These include *Diaphanosoma brevireme*, *Pseudosida ramosa*, *Macrothrix spinosa*, *M.*

elegans, *Chydorus nitidilus*, *Ephemeroporus tridentatus*, *Alona ossiani, Oxyurella ciliata* and *O. longicaudis* (Elías-Gutiérrez 2006). One interesting finding of our study was the presence of *Anthalona brandorffi*, described as *Alona brandorffi* (Sinev & Hollwedel 2002) in the waterbodies Crooked Tree Lagoon, Silvituc Lagoon and Loché, because this species was found for the first time in Boa Vista, Brazil, and its distribution in the Northern Neotropics was unknown. Cladocerans were not as abundant in highland lakes of Guatemala. Laguna de Ayarza and Lake Atitlán still display oligo-mesotrophic conditions. Macrophytes, the typical habitat of cladocerans, are scarce in these lakes. In contrast, Lake Amatitlán is hypereutrophic, and only a single cladoceran species, *Daphnia mendotae*, was collected in such extreme conditions. Species restricted to the highlands include *D. pulicaria* and *S. congener*, even though they apparently have wide distributions (Cerny & Hebert 1993, Illyová & Némethová 2005, Marrone *et al.* 2005). For instance, *D. pulicaria* seems to prefer cool waters, typical of highland Lake Atitlán (≤21.8°C). Occupying cooler, deep waters may be a strategy to reduce risk of predation (Stich & Maier 2007). Species restricted to aquatic ecosystems of Guatemala and Belize include: *Dunhevedia odontoplax* and *Ceriodaphnia dubia*. *Dunhevedia odontoplax* has been collected in Morelos, Veracruz (Elías-Gutiérrez 2006). Mainly cladoceran carapaces were collected in "cenotes" and rivers, but there were few live specimens. Most "cenotes" we sampled lacked aquatic vegetation, the main habitat of most cladoceran species. Distribution of zooplankton in rivers is very heterogenous (Vadadi-Fülöp 2009) and we might simply have collected samples from sites where densities were low. Scarcity of cladocerans in rivers, however, is common because they are not as well adapted to lotic aquatic environments as ostracodes and chironomid larvae. Another explanation for the low species richness and numbers could be that adults of some species are more typical of the rainy season, and we collected surface sediments in the dry

season. Future sampling should be conducted across the seasons.

Only six calanoid copepod species were collected from the sampled waterbodies. Recent studies in Mexico (Elías-Gutiérrez *et al.* 2008, Brandorff 2012) report up to 100 freshwater copepod species, of which 20 species belong to the order Calanoida. Suárez-Morales & Reid (2003) suggest that the fauna of the Yucatán Peninsula has affinities with Cuba and the insular Caribbean, and differs from that of Central Mexico, which is closer to the fauna of upper Central America. *Prionodiaptomus colombiensis* mainly inhabits altitudes from 10 to 100m.a.s.l and it has been previously reported in Tabasco, Mexico while *Leptodiaptomus siciloides* is widely distributed in Mexico (Elías-Gutiérrez *et al.* 2008). *Arctodiaptomus dorsalis* tolerates a broad range of environmental conditions and was collected in waterbodies with different origins and trophic states. For instance, it inhabits hypereutrophic volcanic Lake Amatitlán in the highlands, and meso-oligotrophic, karst Lake Petén Itzá in the lowlands. According to Suárez-Morales (2003), this nearctic species is the most widespread diaptomid in the Yucatán Peninsula and has also been collected in Southeastern USA, central and Eastern Mexico, Central America and the Caribbean islands. Dispersal of this species is relatively recent (post-Pliocene) and it colonized the Yucatán Peninsula during past marine regressions, during times of emergence of areas on the peninsula. This could explain why this species is now highly tolerant and widely distributed.

Of the six copepod species found, *M. reidae* is endemic to Campeche (Elías-Gutiérrez *et al.* 2008, Suárez-Morales & Elías-Gutiérrez 2000) and Northern Guatemala (this study). All species belonging to the genus *Mastigodiaptomus* found in the Yucatán Peninsula are neotropical. Suárez-Morales (2003) report another endemic species for the area, *Mastigodiaptomus maya*. Unfortunately, we did not collect this species, but it seems to coexist with *M. reidae* in Chicaná pond, near the Biosphere Reserve of Calakmul, Yucatán Peninsula, and probably speciated for ecological reasons. Our results indicate that *M. nesus* inhabits waterbodies in Belize, Campeche, Quintana Roo and Yucatán, as reported by Elías-Gutiérrez *et al.* (2008). The present distribution of this taxon could be a remnant of the original *Mastigodiaptomus* fauna in the Yucatán Peninsula and may reflect recent, post-Pliocene dispersal and Holocene climatic fluctuations (Suárez-Morales 2003). We identified *P. marshi* in aquatic ecosystems in the lowlands of Belize (Lagoons Progreso and Almond Hill) in the Eastern lowlands of Guatemala (Lake Izabal) and Southern Yucatán (Bacalar). Pseudodiaptomid copepods mainly inhabit marine and brackish water environments, although recent studies (Suárez-Morales 2003) suggest that *P. marshi* is a species that is starting to colonize freshwater environments. Canonical Correspondence Analysis indicated that the ions sodium and chloride affect the distribution of this species. But the fact that we collected this copepod species in freshwater Lake Izabal supports the idea that is starting to colonize freshwater environments. Lake Izabal is connected with the Caribbean Sea via the Río Dulce and El Golfete. Similar to cladocerans, few copepods were found in rivers, probably because they are not well adapted to inhabit running waters, avoiding such environments and preferring the littoral zones of lakes (Casanova & Henry 2004).

Effects of altitude and related variables precipitation and trophic state, on ostracode species distribution and assemblage composition in the study area are clear. The taxonomy, ecology and distribution of non-marine ostracodes from the Northern Neotropics (Mexico, Guatemala and Belize) was investigated by Pérez *et al.* (2010b, 2010c, 2011b), *Darwinula stevensoni* has a worldwide distribution and *Cytheridella ilosvayi* is abundant throughout the entire continental Neotropics. *Cypridopsis okeechobei* displays a narrower distribution, extending from the United States to the Petén Lake District, Northern Guatemala. *Pseudocandona* sp. was also abundant and we suggest this species is endemic to the Yucatán Peninsula, but further taxonomic and molecular

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analysis is needed to test this assertion. We were unable to identify some ostracodes collected in the highlands to species level. They may be endemic to the region or be distributed throughout higher-elevation areas of Central America and Mexico that have not been studied yet. These species include *Candona* sp., *Limnocythere* sp. and *Trajancypris* sp. A conductivity gradient is well marked on the Yucatán Peninsula. Ostracodes were mainly typical of freshwaters, but some, like *Cyprideis* sp., *Loxoconcha* sp., *Paracytheroma stephensoni*, *Perissocytheridea cribosa* and *Thalassocypria* sp. were typical of waterbodies with high conductivities, up to 55.3mS/cm. *Cypretta brevisaepta* had been reported only from Southern Florida and the West Indies, but we found it in Lakes Oquevix, Macanché, and a pond near Lake Oquevix in Petén, Guatemala and in San José Aguilar, Mexico.

A broad trophic state gradient characterizes the study area, ranging from hypereutrophic Lake Amatitlán to oligotrophic Laguna Ayarza. Hypereutrophic Lake Amatitlán displayed species characteristic of highly productive waters, including *Chironomus anthracinus*, *Discostella* aff. *pseudostelligera*, *Daphnia mendotae*, *Candona* sp., *Cypridopsis vidua* and *Darwinula stevensoni*. Our results demonstrate that few zooplankton and zoobenthos species inhabit higher elevations (>450m.a.s.l.) in Guatemala. Cladocerans, copepods and ostracodes were more diverse and abundant in lowland aquatic ecosystems, suggesting that environmental conditions in those waterbodies are optimal for zooplankton and zoobenthos development and reproduction. The Yucatán Peninsula and surrounding areas (Guatemala and Belize) are rich in aquatic ecosystems, therefore it will be important to collect samples from additional sites to expand our training set. Aquatic bioindicators should also be collected at different seasons to provide information on species life cycles. Despite the utility of the collected data, additional sampling campaigns in aquatic ecosystems throughout Mexico, Guatemala, Belize and Central America are required. We also recommend return visits to previously studied ecosystems to capture seasonal variability. Central Mexico is rich in aquatic ecosystems and there have been few studies on bioindicators in that region. We are developing a calibration dataset for central Mexico that will provide new autecological information for bioindicators that will expand our original Yucatan training set.

Importance of species richness and diversity of bioindicators in neotropical aquatic ecosystems: Diversity and species richness data from waterbodies provide information on modern environmental conditions, e.g., trophic state, anthropogenic impact and urban development and the degree of degradation. Our findings provide information for identifying conservation hotspots on the Yucatán Peninsula, Guatemala and Belize. Highest species diversities were reported at lower elevations (<450m.a.s.l.). The highest number of species and diversities per waterbody were usually reported for lowland lakes, where precipitation is high, up to 3 050mm/y. Crooked Tree Lagoon, Belize displayed the highest diversity ($H \leq 2.4$, diatoms). The lagoon is protected and recognized as a wetland of international importance under the Ramsar Convention of Wetlands (http://www.ramsar.wetlands.org). Lakes Bacalar and Chichancanab, on the Yucatán Peninsula, were declared protected areas in April 2011 (SIPSE 2011). Most aquatic ecosystems in the study area, however, lack such environmental protection. Government agencies, universities and NGOs should collaborate to guarantee that aquatic ecosystems in the region are protected. Highland lakes, despite their lower diversities, deserve special attention because they often possess rare or unidentified taxa and may be home to new or endemic species. Chironomids and ostracodes were highly diverse ($H \leq 2.54$) in sampled aquatic ecosystems. Lakes Chacan Lara, Sabanita and Silvituc were small waterbodies that lacked ostracodes, probably due to low lake water conductivities ($\leq 183 \mu S/cm$). Diatoms, cladocerans and copepods were scarce or lacking in rivers, "cenotes" and coastal waterbodies. Further sampling

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campaigns are needed to corroborate these observations and improve on methods for collection of bioindicators that were present in low abundances. Rivers deserve special attention because they frequently receive domestic and industrial waste, affecting species distributions and diversity.

This study on the waterbodies on and around the Yucatán Peninsula found that microcrustacea, insect larvae and diatoms in neotropical lakes are abundant, diverse and highly sensitive to environmental variables. Such organisms therefore have great potential as modern and late Quaternary bioindicators. This investigation generated the first training sets for chironomids, diatoms, ostracodes, cladocerans and copepods in the region and is a pre-requisite for future quantitative paleolimnological reconstruction of late Quaternary environments in the Northern Neotropics. Our results highlight the exceptional potential of the studied taxonomic groups as bioindicators of climate and trophic state.

Analysis of the distribution and ecological preferences of the five studied groups (diatoms, chironomids, cladocerans, copepods and ostracodes) generated new information that is required to make better use of these aquatic bioindicators in the neotropical region. Clear differences emerged in the chemistry and biology of highland versus lowland water bodies. Volcanic highland lakes display origin and water chemical composition different from those of karst lowland lakes. Biodiversity in the highlands is lower than in the lowlands. The highland aquatic fauna is dominated by chironomids *Apsectrotanypus* sp., *Cricotopus* spp., Tanytarsini C, *Stenochironomus* sp., diatoms *Ulnaria acus*, cladocerans *Ceriodaphnia dubia* and *Bosmina huaronensis*, ostracodes *Candona* sp., *Chlamydotheca colombiensis*, *Cypridopsis vidua*, *Cytheridella ilosvayi*, *Darwinula stevensoni*, *Limnocythere* sp., *Physocypria globula, Stenocypris major* and *Trajancypris* sp, cladocerans *D. pulicaria* and *S. congener* and the copepods *Leptodiaptomus siciloides* and *Prionodiaptomus colombiensis*.

This study covered a wide range of trophic state, which allowed us to differentiate between species that are tolerant and intolerant of highly eutrophic waters. Bioindicator species inhabiting highly productive waters and tolerating extreme conditions include *Chironomus anthracinus*, *Cyclotella meneghiniana*, *Discostella* aff. *pseudostelligera*, *Daphnia mendotae*, *Arctodiaptomus dorsalis*, *Candona* sp., *Cypridopsis vidua* and *Darwinula stevensoni*. A broad conductivity gradient also characterizes the Yucatán Peninsula and surrounding areas. Most collected species inhabit freshwaters, but a few tolerate high conductivities, making them potential indicators of such conditions. They include diatoms such as *Halamphora coffeaeformis*, *Campylostylus normannianus*, *Nitzschia frustulum*, *Navicula palestinae*, *Tabularia fasciculata*, *Navicula salinarum*, *Amphora securicula*, and *Cocconeis placentula*, cladocerans *Simocephalus mixtus* and *Karualona muelleri*, the copepod species *P. marshi*, as well as ostracodes *Cyprideis* sp., *Perissocytheridea cribosa* and *Thalassocypria* sp. Good indicators of alkaline waters are *Paratanytarsus* sp.1, *Djalmabatista* sp., *Endotribelos* sp., and *Mastigodiaptomus nesus*, whereas waters with $HCO_3 < 275mg/L$ were dominated by *Stempellina* sp., Tanytarsini J, K, *Apedilum* sp and *Arctodiaptomus dorsalis*.

Transfer functions that express quantitative relations between bioindicator species and environmental variables will ultimately be developed using results from this study. These transfer functions will be used to make quantitative paleoenvironmental inferences, by applying them to fossil assemblages in sediment cores retrieved from lakes in the region. Despite the utility of the collected data, additional sampling campaigns in aquatic ecosystems throughout Mexico, Guatemala, Belize and other parts of Central America are required. We also recommend return visits to previously studied ecosystems to capture seasonal variability.

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RESUMEN

Los quironómidos, diatomeas y microcrustaceos que habitan ecosistemas acuáticos en el norte de los Neotrópicos son abundantes y diversos. Algunas especies son altamente sensibles a cambios en la composición química del agua y en el estado trófico. Este estudio se realizó como el primer paso para desarrollar funciones de transferencia para inferir condiciones ambientales en el norte de las tierras bajas de los Neotrópicos. Es por esto que las abundancias de especies bioindicadoras se relacionaron con múltiples variables ambientales con el fin de explotar al máximo su uso como indicadores ambientales y paleoambientales. Recolectamos y analizamos muestras de agua y de sedimento superficial de 63 cuerpos de agua, ubicados a lo largo de un gradiente trófico y de gradientes marcados de altitud (~0-1 560m.s.n.m.) y de precipitación (~400-3 200mm/año), desde el NO de la Península de Yucatán (México) hasta el sur de Guatemala. Relacionamos 14 variables limnológicas con las abundancias relativas de 282 especies de diatomeas, 66 morfoespecies de quironómidos, 51 especies de cladóceros, 29 especies de ostrácodos no-marinos y seis especies de agua dulce de cladóceros calanoides. La estadística multivariada indicó que el bicarbonato es el principal determinante de la distribución de quironómidos y copépodos. El estado trófico es el segundo factor más importante en determinar la distribución de quironómidos. La conductividad, que está relacionada con el gradiente de precipitación e influencia marina en la Península de Yucatán, es la principal variable en influir las comunidades de diatomeas, ostrácodos y cladóceros. Las diatomeas, quironómidos y cladóceros (H=2.4-2.6) presentaron diversidades más altas que los ostrácodos y copépodos (H=0.7-1.8). La riqueza de especies y la diversidad fueron más altas en las elevaciones bajas (<450m.s.n.m) que en elevaciones altas en Guatemala. La distribución y diversidad de bioindicadores es afectada por múltiples factores incluyendo la altitud, precipitación, composición química del agua, estado trófico y el impacto humano.

Palabras clave: microcrustáceos, quironómidos, diatomeas, ecosistemas acuáticos, norte de los Neotrópicos, autecología, diversidad.

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