Geodiversity influences limnological characteristics and freshwater ostracode species distributions across broad spatial scales in the northern Neotropics

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Abstract. Geodiversity is recognized as one of the most important drivers of ecosystem characteristics and biodiversity globally. However, in the northern Neotropics, the contribution of highly diverse landscapes and geological history in structuring large-scale patterns of aquatic environments and aquatic species associations remains poorly understood. We evaluated the relationships among geodiversity, limnology and freshwater ostracodes from southern Mexico to Nicaragua. Cluster analysis, based on geological, water-column physical and chemical variables, and geochemical and mineralogical characteristics of 76 aquatic ecosystems (karst, volcanic, tectonic) revealed two main limnological regions: (1) karst plateaus of the Yucatán Peninsula and northern Guatemala, and (2) volcanic terrains of the Guatemalan highlands, mid-elevation sites in El Salvador and Honduras, and the Nicaraguan lowlands. In addition, seven subregions were recognized, demonstrating a high heterogeneity of aquatic environments. Principal Component Analysis identified water chemistry (ionic composition) and mineralogy as most influential for aquatic ecosystem classification. Multi-parametric analyses, based on biological data, revealed that ostracode species associations represent disjunct faunas. Five species associations, distributed according to limnological regions, were recognized. Structural equation modelling (SEM) revealed that geodiversity explains the limnological regions and subregions of the study area. Limnology further explained species composition, but not species richness. The influence of conductivity and elevation were statistically significant for ostracode species composition, though not for species richness. We conclude that geodiversity has a strong influence on the limnological characteristics of aquatic systems, which, in turn, influence ostracode species composition in lakes of the northern neotropical region.

1 Introduction

Geodiversity is defined as the natural variety of geological, geomorphological, and hydrological features of a landscape (Gray, 2019). Geodiversity reflects aspects of regional or local climate, hydrology, and soil properties (Vartanyan, 2006a; Hu et al., 2020). By interacting with the biosphere and the atmosphere, geodiversity can also contribute, through sediment delivery, to the input of nutrients into ecosystems, and determine the chemical composition of environments (Vartanyan, 2006b; Bravo-Cuevas et al., 2021). Geodiversity has been fundamental for ecosystem development and biological evolution at scales ranging from local to global (Mittelbach et al., 2007; Etienne and Apol, 2009; Smith et al., 2010; Bryson et al., 2013; Gillespie and Roderick, 2014; Steinbauer et al., 2016).

Biological diversity, defined as the variety of life forms in a place on Earth (Huston, 1995), is strongly related to geodiversity, as species are distributed in response to landscape features. Biological diversity is dynamic. Species evolve and distribution patterns change at rates different from rates of change of geodiversity. This suggests that other intrinsic (e.g., ecological) and extrinsic (e.g., climate) factors, either ancient or recent, have interacted to shape regional species pools. In areas with highly dynamic and complex biological systems, such as tropical regions (Rull, 2011; Antonelli et al., 2018; Matzke-Karasz et al., 2019; Moguel et al., 2021), it is difficult to discern the contributions of individual versus joint factors that shaped the distribution of past and modern biota (Rossetti and Toledo, 2016). Understanding the role of geodiversity in the structure of biological systems is key to identifying evolutionary traits and mechanisms that control species distributions, and can be applied to conservation, ecosystem management, and prediction of ecosystem responses to future climate scenarios (Martiny et al., 2006; Hulsey et al., 2010; Jiménez-Alfaro et al., 2018).

The northern Neotropical region extends from central-southern Mexico to Central America and includes the Caribbean. It is characterized by a dynamic geological history, caused by the interplay of the North American, Cocos and Caribbean tectonic plates (Molnar and Sykes, 1969; Marshall, 2007). The region is characterized by broad ranges of elevation and soil types, displays frequent volcanic and seismic activity, and has been subjected to repeated marine regressions and transgressions (Brezonik and Fox, 1974; Horn and Haberyan, 1993; Umaña et al.,1999; Haberyan et al., 2003; Obrist-Farner et al., 2021). At least 16 biogeographic provinces are recognized, based on terrestrial plant and animal taxa (Morrone, 2014).

Numerous studies have attempted to elucidate the relationship between geodiversity and biological diversity and identify the factors that account for the current biogeographic patterns in the northern Neotropics (Wallace, 1853; Patton et al., 1994; Gillespie and Roderick, 2014). Most evidence from terrestrial taxa suggests *in situ* diversification, resulting from repeated colonization events by North and South American taxa, before and after the closure of the Isthmus of Panama, estimated to have occurred between 15 and 4 Mya (Bacon et al., 2015; Montes et al., 2015). Molecular evidence suggests that extant Mesoamerican terrestrial taxa (i.e., angiosperms, ferns, birds, reptiles and mammals) originated primarily in the Amazon Basin, with ancestors arriving by dispersal during the last 10 Mya (Antonelli et al., 2018).

These large-scale species movements between the American continents were mainly associated with large-amplitude Pleistocene climate fluctuations such as glacial and interglacial cycles and episodes of shorter, centennial to millennial fluctuations, such as Late Glacial Heinrich and Dansgaard-Oeschger stadials (Behling et al., 2000; Carnaval and Moritz, 2008; Bouimetarhan et al., 2018; Baker et al., 2001, 2020). It is therefore assumed that both geodiversity and climate change have been fundamental in shaping the current patterns of species diversity and distribution of terrestrial taxa (Haffer, 1969; Wiens and Donoghue, 2004; Peterson and Nyári, 2008; Smith et al., 2012; Leite et al., 2016).

In aquatic environments of the northern Neotropics, diversification and drivers of species distribution are less well known than those that operated in terrestrial environments. For instance, most aquatic species have dispersal limitations generated by system morphologies and environmental variables, such as sediment texture, geochemistry, and water physico-chemical properties, and how they have been modified through time (Albert and Reis, 2011; Bagley and Johnson 2014; Cabassi et al., 2019). The limnology of a region, defined as the set of physical, chemical, and biological components of inland waters, and its interactions with terrestrial, atmospheric, anthropogenic, and geological elements, in a spatial and temporal framework (Last, 2002; Azim, 2009; McCullough et al., 2021), is generally accepted as a fundamental driver of the diversification and distribution of aquatic species (Matamoros et al., 2015). The relevance of limnology for recent or past biological community composition and species richness in the northern Neotropics, however, has been poorly evaluated.

During the last 50 years, anthropogenic influences on aquatic environments have altered biological diversity and species distributions because of the modification of natural conditions (Albert and Reis, 2011; Wehrtmann et al., 2016; Franco-Gaviria et al., 2018). Currently, most aquatic environments in the northern Neotropics are used as potable water sources and for agriculture; in large lakes, fishing and aquaculture have caused eutrophication and introduced invasive species (e.g., *Oreochromis niloticus*). In addition, some lakes located close to urban centers and farmlands are used as disposal sites for waste waters, agrochemicals, and mine residues (McKaye et al., 1995; Soto et al., 2020). The high heterogeneity of geodiversity in the northern Neotropics, and the poor knowledge of the limnological attributes of aquatic ecosystems in the region make it difficult to: (1) understand the complex relations among geology, water-column physico-chemical variables and biological characteristics (community composition and species richness) and (2) distinguish different limnological regions and determine their geographic coverage. There is great uncertainty about how geodiversity and limnological variables influenced aquatic biota over time, and what factors have determined current patterns of diversity and distribution.

Freshwater ostracodes are a well-suited group to evaluate past and present drivers of species distribution in the northern Neotropics. Ostracodes are bivalved microcrustaceans that are abundant, diverse, and widely distributed in aquatic ecosystems (Pérez et al., 2011b, 2013a; Cohuo et al., 2016, 2020; Macario-González et al., 2018; Echeverria-Galindo et al., 2019). This taxonomic group shows levels of endemism (restricted distribution) as high as 74%, sometimes confined to a single lake, or found in surface waters throughout the region (Cohuo et al., 2016). In sediment sequences from lakes of the northern Neotropics, ostracode remains are abundant, particularly in late Pleistocene deposits (Pérez et al., 2011b, 2013a; Cohuo et al., 2020). The greatest limitation for using freshwater ostracodes to identify drivers of species distribution in the northern Neotropics is the scarcity of integrated and comparable regional studies, for which detailed spatial and temporal limnological and biological data were collected.

We conducted a limnological and biological survey of aquatic systems across the northern Neotropics, from southeast Mexico to Nicaragua, to obtain environmental data across broad spatial scales to answer two main questions: (1) To what extent does geodiversity control limnological variables and thus define limnological regions?; (2) how does geodiversity (water and sediment geochemistry characteristics, as influenced by geology) affect diversity and distributions of ostracode species?

2. Materials and Methods

2.1. Study area

Our study area covers the northernmost Neotropics, ranging from southern Mexico (Yucatán Peninsula) to Nicaragua (Fig. 1). This region is considered a biodiversity hotspot (Mesoamerican hotspot; Myers et al., 2000), with more than 5000 endemic vascular plants (De Albuquerque et al., 2015), and about 1120 bird (~200 endemic), 440 mammal (65 endemic), 690 reptile (~240 endemic), 550 amphibians (~350 endemic), and 500 fish species (~350 endemic) (CEPF, 2021). Species from North and South America converge in this region (Myers et al., 2000; Ojeda et al., 2003; DeClerck et al., 2010; Rull, 2011). The orography is highly irregular, and elevations range from sea level to more than 4500 m a.s.l. (Molnar and Sykes, 1969; Marshall et al., 2003, 2007). Plate tectonic interactions are responsible for active volcanism along the Central American Volcanic Arc and high seismic activity (Marshall et al., 2003, 2007). The climate is typically tropical (Köppen-type group A-climate “tropical/megathermal climate”, Peel et al., 2007) and predominantly warm at low elevations (26°C mean annual temperature) (Waliser et al., 1999). Because of the irregular orography, at least a dozen climate sub-zones are distinguished (Taylor and Alfaro, 2005). Mean annual precipitation in the study area ranges from <500 to >3000 mm and is highly seasonal, governed by the seasonal migration of the Intertropical Convergence Zone (ITCZ). The northern position of the ITCZ during summer results in the so called “rainy season,” during which precipitation increases from ~240 mm in April to more than 1600 mm in September-October (Hastenrath, 1967; Magaña et al., 1999). The hurricane season extends from July to December and is an important contributor to the humidity budget because on average, 300 mm day^{-1} of rain falls during tropical storms and hurricanes (Jury, 2011). The region is rich in aquatic systems that are of different origins, shapes, and hydrological dynamics, as well as water chemistry and sediment composition. The karst Yucatán Peninsula, for example, with about 8000 *cenotes* (sinkholes), many lakes, and both surface and subterranean rivers, is considered a unique hydrological region (Schmitter-Soto et al., 2002a, Alcocer and Bernal-Brooks, 2010). In Central America, lakes and wetlands cover more than 8% of the total land area (Ellison, 2004). Most important aquatic ecosystems in the northern Neotropics include coastal, tectonic and volcanic lakes, such as crater lakes and maars, karst waterbodies including lakes, *cenotes* and *aguadas* (water accumulated in topographic depressions under canopy cover), flooded caves, subterranean rivers, and both permanent and ephemeral ponds (Brezonik and Fox 1974; Pérez et al., 2011a; Delgado-Martínez et al., 2018; Echeverría-Galindo et al. 2019; Obrist-Farner and Rice, 2019).

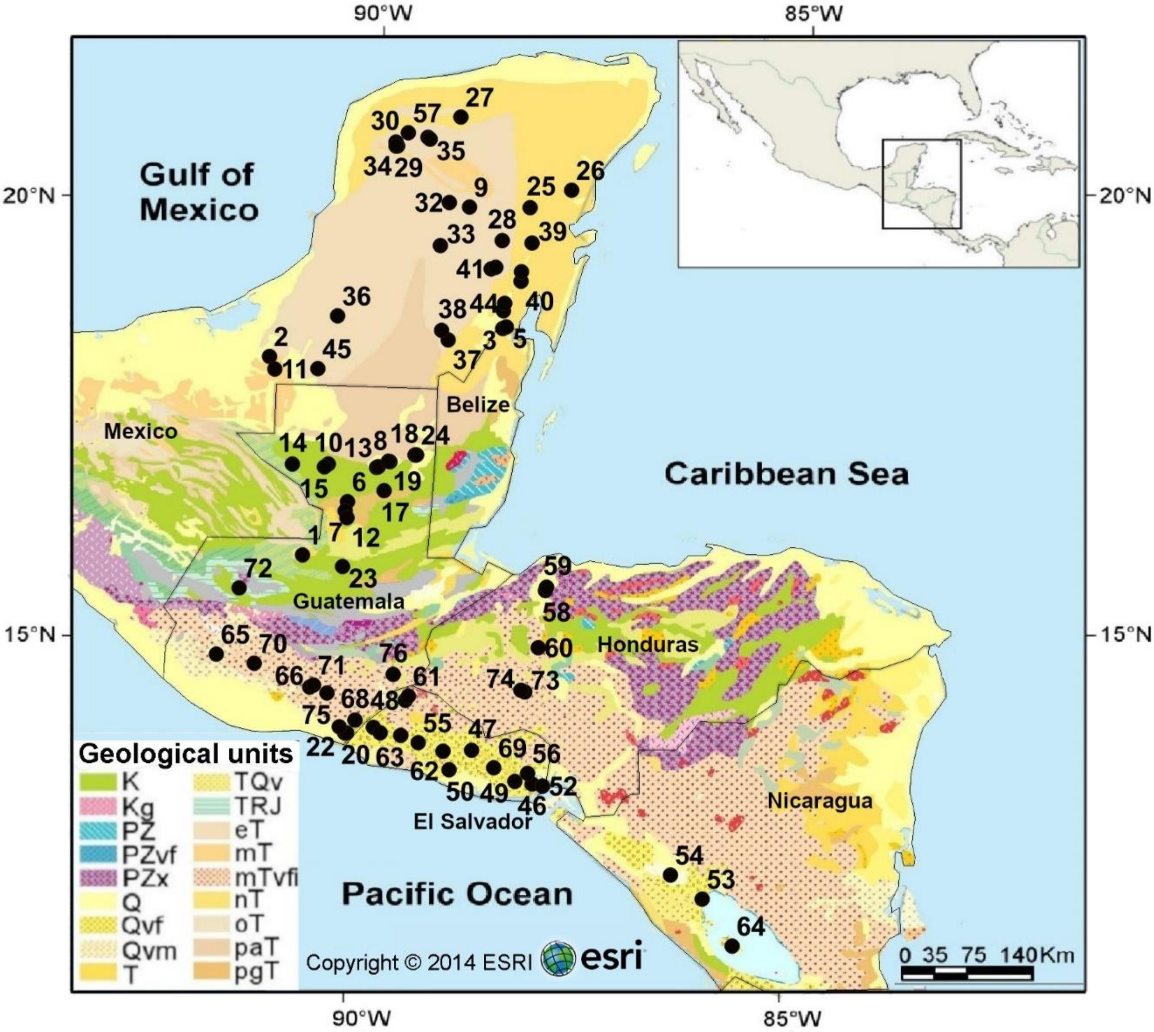

Figure 1: Simplified geological map of the northern Neotropical region showing the locations of the 76 studied aquatic ecosystems. Colors indicate geological units based on bedrock type and age of the sediments. Geological data were obtained from Garrity and Soller (2009). Black dots and numbers represent sampling localities. Detailed information on sampling sites can be found in Table 1. Legend: K_ Cretaceous sedimentary rocks; Kg_ Cretaceous Plutonic rocks; PZ, PZvf, PZx_ Paleozoic sedimentary rocks; Q_ Quaternary sedimentary rocks; Qvf, Qvm, TQv_ Quaternary volcanic rocks; T_ Tertiary sedimentary rocks of undetermined age; TRJ_ Jurassic sedimentary rocks; eT_ Eocene sedimentary rocks; mT_ Miocene sedimentary rocks; mTvfi_ Miocene volcanic rocks; nT_ Eocene sedimentary rocks; oT_ Oligocene sedimentary rocks; paT, pgT_ Paleocene sedimentary rocks.

2.2. Sampling aquatic environments in the northern Neotropics

A total of 76 aquatic ecosystems located in five countries across the northern Neotropical region (Fig. 1) were sampled during July-October 2013, coinciding with the rainy season in the region. These systems are situated on the Yucatán Peninsula, Mexico (n=28), Guatemala (n=26), El Salvador (n=14), Honduras (n=5) and Nicaragua (n=3) (Fig. 1). For all water bodies, physical and chemical variables (temperature, dissolved oxygen, pH, conductivity) were measured *in situ* with a WTW Multi Set 350i multi-parameter probe at a water depth of 0.5 m. Maximum water depth at each site was measured with an echosounder Fishfinder GPSMAP 178C. Location of sites, including elevation, latitude, and longitude, was determined with a navigator Garmin GPSmap 60c.

Water samples for analysis of major anions (Cl^-, SO_4^{2-}, CO_3^{2-}, HCO_3^-) and cations (Ca^{2+}, K^+, Mg^{2+}, Na^+) were collected at water depths of 0.5 m below surface using a Ruttner-type water sampling bottle. All water samples were filtered *in situ* using a 0.45-µm pore size Whatman glass microfiber filter. For cation analysis, filtered samples were acidified with HNO_3 to pH 2. Waters were stored under refrigeration until analysis.

Biological samples were collected from the littoral zone and deepest area of the profundal zone. In littoral areas, we collected a maximum of five samples per aquatic ecosystem, using a 250-µm-mesh hand net. Collection sites were distributed at regularly spaced intervals across the systems and were mostly characterized by submersed vegetation. A maximum of five surface sediment samples per aquatic ecosystem were collected from the deepest area with an Ekman grab, and the uppermost 3 cm of each grab were used for analysis.

2.3 Environmental variables: water chemistry, sediment geochemistry, mineralogy, and geology

Water chemistry analysis: Ionic composition was analyzed following Armienta et al. (2008). Bicarbonate was measured by acid titration to pH 4.6, using a mixed indicator of methyl red and bromocresol green. Concentrations of calcium and magnesium were obtained by complexometric titration with EDTA, whereas sodium and potassium were measured by atomic emission spectroscopy. Chloride was potentiometrically determined using an ion selective electrode, adding a 5 M solution of $NaNO_3$ as an ionic strength adjuster. Sulfate was determined by turbidimetry. Analytical quality was checked by ionic charge balance and most samples were balanced, with < 5% error. Major ions concentrations are expressed in mg L^{-1}, but the data were transformed to meq L^{-1} and percentages to determine anion and cation dominance and water type and test the charge balance. Sodium and potassium were summed. Ternary plots were constructed using the PAST 4.03 software (Hammer et al., 2001).

Geochemical analysis: Total carbon (TC) and total nitrogen (TN) contents in sediments were determined by combustion under oxygen saturation with a LECO TruSpec Macro CHN analyzer. Total inorganic carbon (TIC) was quantified with a Woesthoff Carmhograph C-16 after dissolution with phosphoric acid (45% H_3PO_4) and detection of the CO_2-induced conductivity change in NaOH. Total organic carbon (TOC) was calculated by subtracting TIC from TC.

Mineralogical analysis: Qualitative and semi-quantitative mineralogical compounds in sediments were examined by x-ray diffraction with a RIGAKU Miniflex600. For the identification and semi-quantification of the minerogenic components, the software Philips Highscore was used. All sediment analyses used are described in detail in Vogel et al. (2016).

Geological analysis: The geological map of North and Central America generated by the Geological Society of America (GSA) (Reed et al., 2005) and adapted and converted to a geographic information system (GIS) by Garrity and Soller (2009), was used to identify geological regions in our study area. ArcGIS software was used to identify geological attributes of sampling sites such as bedrock type and age of sediments. Three major types of bedrock were distinguished: sedimentary, volcanic and plutonic rocks. Ten geologic periods and epochs, respectively, were defined: Jurassic, Cretaceous, Tertiary of undetermined age, Paleogene of undetermined age, Paleocene, Eocene, Oligocene, Neogene of undetermined age, Miocene, and Quaternary.

2.4 Limnological regionalization using cluster analysis and PCA

The final data set includes 23 variables, of which 21 are numerical and the remaining two are categorical (Table S1). Numerical variables include elevation, water physical and chemical properties (temperature, dissolved oxygen, pH, conductivity, CO_3^{2-}, HCO^{3-}, SO_4^{2-}, Cl^-, Na^+, K^+, Ca^{2+} and Mg^{2+}), sediment geochemistry (total carbon (TC), total inorganic carbon (TIC), total organic carbon (TOC), total nitrogen (TN)) and mineralogy (quartz, carbonate, phyllosilicates, and feldspars). Categorical data are geological properties represented by bedrock type and age of sediments.

Prior to statistical analysis, numerical data were log-transformed, except for pH, which is already a log-transformed value, to achieve an approximate normal distribution of variables. Normality was verified for all variables using the Shapiro-Wilk test. Missing data were substituted with the mean value of the respective variable, as missing values represented < 8% of the data set (Jakobsen et al., 2017).

We performed a cluster analysis (CA) to define groups of lakes based on the similarity of their measured attributes. For this analysis, we included all numerical variables. We used the unweighted pair group method with arithmetic mean (UPGMA) for the CA, and Euclidean distance to investigate the grouping similarity of sampling points. Calculations were conducted in R software (R Development Core Team, 2015), using the Vegan package (Oksanen et al., 2017).

We then used a Principal Component Analysis (PCA) for each of the main groups discriminated by the cluster, to identify correlated and explanatory variables of the data sets. For each group, the first PCA run included all 23 variables measured (numerical and categorical) and those represented by superimposed arrows in the graphs were considered correlated and excluded from further statistical analysis. A second PCA run, using uncorrelated variables, was used to identify explanatory variables of the data sets. The PCA mix package implemented in R software (Chavent et al., 2014) was used because of its ability to handle quantitative and categorical data simultaneously. The loading values for all parameters were obtained using normalized rotation.

To provide a graphical representation of the most meaningful variables of the data sets detected in the PCA, and further evaluate latitudinal and/or altitudinal environmental gradients, we created an environmental variable-specific map using kriging interpolation. We used an empirical semi-variogram to quantify the spatial composition and structure of the data (Wagner, 2003; Bivand et al., 2008). We then fitted a theoretical variogram using the nugget effect (0.5), and a partial sill (0.5) in a linear model. We ultimately obtained a map representing measured data and estimates from unmeasured locations. The software Surfer® from Golden Software, LLC (www.goldensoftware.com) was used for calculations.

2.5. Biological analysis: ostracode abundances, identification, and statistics

Ostracode extraction and counting was carried out using 15 cm^3 of wet sediment. Specimens were picked using a stereomicroscope Leica MZ75. Only adult specimens, represented by single valves, empty carapaces or complete organisms (carapace and soft body) were counted. Species identification was undertaken using three individual adult specimens with complete soft parts of each morphotype identified. Identification using more than a single organism is appropriate in ostracodes, given morphological plasticity and mutations that can modify morphology. Specimens were dissected using distilled water and glycerin (3%) under a stereomicroscope. Selected shells from identified species were photographed with a Zeiss Axio Imager 2 microscope. Shells were stored in micropaleontology slides. Dissected soft parts were mounted on individual slides with Hydromatrix®. Species-level identification was conducted using species keys provided by Karanovic (2012). When keys did not fully resolve taxonomic identities, original descriptions were consulted. Taxonomic classification follows Cohuo et al. (2016). Undissected material was preserved in Eppendorf plastic vials with 70% ethanol and is currently available at the ostracod collection of the Instituto Tecnológico de Chetumal, Mexico. Shannon diversity index, used for species diversity metrics, was calculated with PAST 4.03 software (Hammer et al., 2001).

Ostracode species associations: Species associations were examined by means of non-metric multidimensional scaling (NMDS) (Legendre and Legendre, 1998). This procedure generates an ordination in a two-dimensional space, representing the pairwise dissimilarity between species according to their occurrences. We used the Bray-Curtis dissimilarity coefficient on a presence-absence database (Sørensen Coefficient), as count data were highly heterogenous (with species presence in subsets of samples and absences in most of the database), to which NMDS is sensitive. Only species with at least two occurrences were included in this analysis. In NMDS graph, species associations were determined with a hierarchical cluster analysis based on Ward distances. To test significance between species groups discriminated in NMDS, a permutational multivariate analysis of variance (PERMANOVA) was performed. We used a permutation with 9999 replicates and applied the Bonferroni correction. Calculations were done with R software, using the Vegan package (Oksanen et al., 2017).

Relating environmental variables and ostracode abundances: The relative importance of geochemical, mineralogy, and water physical and chemical conditions for ostracode species composition and distribution was assessed by multivariate constrained ordination techniques. We use ostracode relative abundance and uncorrelated variables for calculations. First, we performed a Detrended Correspondence Analysis (DCA) with detrending by segments and non-linear rescaling to estimate the extent of the environmental gradient (Hill and Gauch, 1980) and to decide which type of ordination would be more appropriate for our data set. Species–environmental relationships were then analyzed using Canonical Correspondence Analysis (CCA) (Ter Braak, 1986). Environmental variables were standardized and added by forward selection using the Monte Carlo permutation test with 999 permutations ($\alpha = 0.05$). Calculations and final ordination graphs of the DCA and CCA were performed using the software Canoco version 5 (Šmilauer and Lepš, 2014).

2.6. Structural equation modeling

To disentangle the relationships between geodiversity, limnology and species composition (as a function of distribution) and richness we used structural equation modeling (SEM). This is a multivariate statistical technique that enables one to model pre-defined causal relationships between observed and non-observed (latent) variables and test their statistical significance (Fan et al., 2016; Sarstedt and Ringle, 2020). Our conceptual model for SEM was based on the assumption that geodiversity in the northern Neotropics is heterogenous, relatively constant in the Yucatán Peninsula and Guatemalan lowlands, but highly variable in the rest of our study area (Guatemalan highlands-Nicaragua). Aquatic systems are, consequently, partially, or entirely influenced by underlying geodiversity, and thus environmental variables such as sediment geochemistry and mineralogy, water ionic composition, temperature, and conductivity of lake waters (limnology) are modified in response to geodiversity changes. At the regional scale, geodiversity and limnology are expected to exert a direct or indirect influence on ostracode species richness and community composition. The individual influence of variables forward selected in the CCA as explanatory for species-environment relationships, and those that may display environmental gradients such as elevation, conductivity, and TOC, were also tested in the models evaluated.

For this conceptual framework, ‘geodiversity’ (latent and exogenous variable) was constructed with all or a subset of geological (bedrock type and age and elevation) and mineralogical variables. ‘Limnology’ (latent and endogenous variable) was constructed using geochemistry (TOC), and water physical and chemical (major anion and cation, temperature, pH, and conductivity) variables. Species richness was treated as an observed variable, and the latent variable ‘species composition’ was constructed using NMDS associations. Using a covariance matrix with a set of uncorrelated variables, we fitted five models using this conceptual framework. For all models, statistical significance was tested with Root Mean Square Error of Approximation (RMSEA), comparative fit index (CFI) and standardized root mean squared residuals (SRMR). The predictive power of the model (R-square) was measured based on the amount of variation of the biological data. The most parsimonious model fitting our data set was selected as the explanatory model (Sect. S1 in the Supplement). The software R and the package Lavaan (Rosseel, 2012) were used for calculations.

3 Results

3.1 Limnological regionalization in the northern Neotropics

Cluster analysis identified two main groups that represent limnological regions (Fig. 2). The first group (YG: Yucatán and Guatemala) consists of lowland lakes from the Yucatán Peninsula (Mexico), the Petén district (northern Guatemala) and the Pacific lowlands of southern Guatemala. The second group (GSHN: Guatemala, Salvador, Honduras, Nicaragua) consists of Guatemalan highland lakes, El Salvador and Honduras mid-elevation lakes and Nicaraguan lowland lakes.

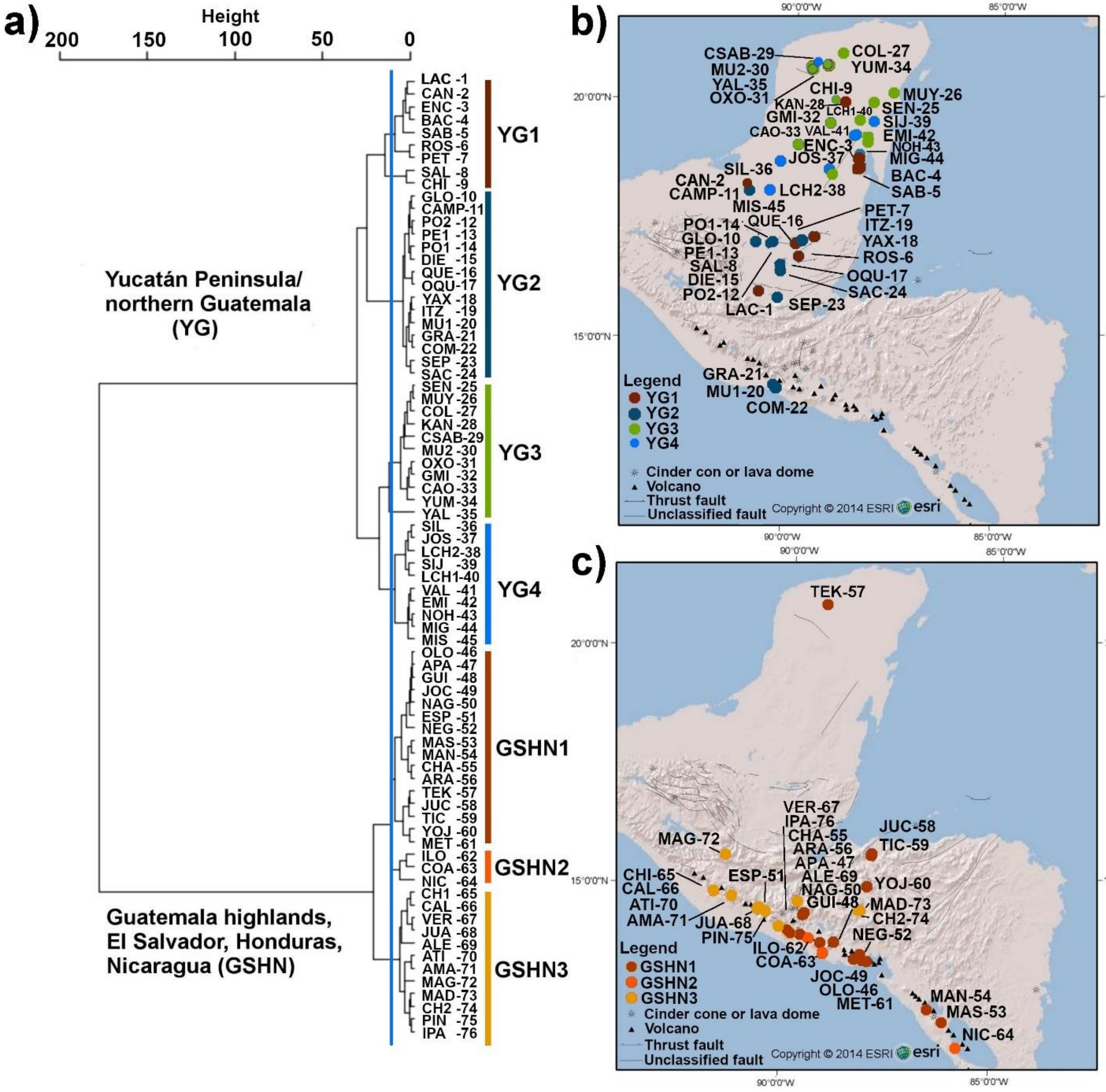

Figure 2 (a) Cluster analysis dendrogram of the 76 studied aquatic ecosystems using 23 water physico-chemical, sediment geochemistry, mineralogical, and geological variables. Blue line indicates cut-off criterion for cluster partition. Two major groups and seven subgroups were detected and named according to their position in the study area: Yucatán Peninsula/Northern Guatemala (YG) and Guatemala highlands, El Salvador, Honduras, Nicaragua (GSHN). In order to provide a graphic representation of cluster grouping, a color bar was assigned to each group and lakes within these groups were plotted on (b) YG map and (c) GSHN map using the same color. Lake full names of codes presented in cluster and maps are given in Table 1. Numbers of lake name codes correspond to that in Figure 1.

Table 1 shows a list of all the studied aquatic ecosystems located in the YG and GSHN limnological regions and subregions, as well as information about selected attributes determined in this study. Detailed results of water physico-chemical, geochemical, mineralogical, and geological analyses for all studied water ecosystems can be founded in Table S1.

Table 1. Limnological classification of 76 aquatic ecosystems of the northern Neotropical region, with their main water physico-chemical, mineralogical, and geological properties.

Limnology		Country	Site		ID	Coordinates		Origin	Elevation (m.a.s.l)	Surface area (km^2)	Depth [a] (m)	Water type (ionic dominance)	Dominant minerals in sediment
group	Sub group		number	Site		N	W						
YG	YG1	GUA	1	Lachuá	LAC	15.92	90.6732	tectonic	170	4	378	SO4<<HCO3--Ca	Calcite
		MEX	2	Candelaria River	CAN	18.181	91.0493	Tectono-karstic	32	river	1.8	HCO3<<SO4--Ca	Calcite
		MEX	3	Encantada	ENC	18.499	88.3895	karst	4	0.07	3	SO4--Ca<<Mg	Calcite
		MEX	4	Bacalar	BAC	18.701	88.3819	karst	4	51	16	SO4--Ca<<Mg	Calcite
		MEX	5	Sabana de Chetumal	SAB	18.517	88.3488	karst	7	0.88	1.6	SO4--Ca--Mg	Nd
		GUA	6	El Rosario	ROS	16.526	90.1601	karst	126	0.02	3	HCO3<<SO4--Ca<<Mg	Dolomite
		GUA	7	Petexbatún	PET	16.421	90.1862	tectono-karstic	120	5.6	40	HCO3<<SO4--Ca<<Mg	Calcite
		GUA	8	Salpetén	SAL	16.981	89.6755	tectono-karstic	105	2.77	10	SO4--Ca--Mg	Calcite
		MEX	9	Chichancanab	CHI	19.884	88.7682	tectonic	1	5.1	15	SO4--Ca<<Mg	Calcite
	YG2	GUA	10	La Gloria[b]	GLO	16.955	90.3789	tectono-karstic	138	3.6	65	SO4<<Cl--Ca	Nd
		MEX	11	Camp	CAMP	18.037	90.9887	Flooded depression	43	2.59	3.5	SO4<<Cl--Ca	Nd
		GUA	12	Las Pozas	PO2	16.343	90.1660	karst	152	2.16	35	HCO3--Mg<<Ca	Nd
		GUA	13	Petenchel	PE1	16.916	89.8288	tectono-karstic	118	0.73	Nd	HCO3--Ca	Phyllosilicates
		GUA	14	Poza azul	PO1	16.954	90.7884	karst	160	0.08	78.1	HCO3--Mg<<Ca	Nd
		GUA	15	San Diego[b]	DIE	16.922	90.4231	tectono-karstic	156	3.8	8.1	SO4<<Cl--Ca	Nd
		GUA	16	Quexil	QUE	16.923	89.8099	tectono-karstic	120	2.2	25.5	HCO3--Ca	Nd
		GUA	17	Oquevix	OQU	16.651	89.7427	karst	150	1.6	10	HCO3--Ca	Quartz
		GUA	18	Yaxhá	YAX	17.058	89.3897	tectono-karstic	164	7	22	HCO3--Ca	Quartz and

													phyllosilicates
		GUA	19	Peten Itzá[b]	ITZ	16.986	89.6938	tectono-karstic	112	100	165	SO4<<HCO3--Ca<<Mg	Nd
		GUA	20	El muchacho	MU1	13.889	90.1918	Flooded depression	3	0.36	2	HCO3<<Cl--Na<<Ca	Feldspars
		GUA	21	Grande	GRA	13.890	90.1703	Flooded depression	5	0.95	2	HCO3--Mg<<Ca	Phyllosilicates
		GUA	22	Comandador	COM	13.960	90.2544	Flooded depression	20	0.65	1.7	HCO3--Ca--Mg	Phyllosilicates
		GUA	23	Sepalau	SEP	15.786	90.2167	karst	266	0.03	10.3	HCO3--Ca	Quartz and phyllosilicates
		GUA	24	Sacnab	SAC	17.058	89.3725	tectono-karstic	170	4.28	9	HCO3--Ca	Quartz and phyllosilicates
	YG3	MEX	25	Señor	SEN	19.876	88.0775	karst	3	1.06	2	Cl<<SO4--Na<<Mg	Calcite
		MEX	26	Muyil	MUY	20.075	87.6037	karst	-1	2.52	16	Cl<<HCO3--Na--Mg	Calcite
		MEX	27	Colac	COL	20.909	88.8669	karst	11	0.0002	120	Cl<<HCO3--Na--Mg--Ca	Calcite
		MEX	28	Kaná	KAN	19.501	88.3954	Flooded depression	5	1.01	2.5	HCO3<<SO4--Na--Ca	Nd
		MEX	29	Sabak-ha	CSAB	20.580	89.5881	karst	18	0.0002	90	HCO3<<Cl--Na<<Ca	Calcite
		MEX	30	Mucuyche	MU2	20.624	89.6065	karst	17	Cavern	18	Cl<<HCO3--Na--Ca	Ankerite
		MEX	31	Oxolá	OXO	20.678	89.2417	karst	18	Cavern	16	HCO3<<Cl--Ca--Mg	Calcite
		MEX	32	San Miguel	GMI	19.935	88.9983	karst	32	Cavern	1.2	HCO3<<Cl--Ca--Mg-Na	Calcite
		MEX	33	Caobas	CAO	18.445	89.1006	Flooded depression	126	0.13	4	HCO3<<SO4--Ca	Calcite
		MEX	34	Yumku	YUM	20.578	89.6052	karst	16	Cavern	15	HCO3<<Cl--Ca--Mg--Na	Calcite
		MEX	35	Yalahau	YAL	20.657	89.2170	karst	2	0.25	12	Cl<<HCO3--Na--Mg	Nd
	YG4	MEX	36	Silvituc	SIL	18.643	90.2727	unknown	69	7.9	3	HCO3--Ca<<Na	Quartz and phyllosilicates
		MEX	37	San José de la Montaña	JOS	18.369	89.0120	karst	118	2	3	HCO<<Cl--Na<<Ca	Nd

		MEX	38	Chacanbacab	LCH2	18.478	89.0869	Flooded depression	109	257.29	3	HCO3--Ca<<Na	Phyllosilicates
		MEX	39	Sijil Noh ha	SIJ	19.473	88.0554	karst	0	0.25	8	SO4<<Cl--Na--Mg	Nd
		MEX	40	Chacchoben	LCH1	19.037	88.1811	Flooded depression	6	0.57	4	HCO3<<Cl--Ca<<Na	Nd
		MEX	41	Vallehermoso	VAL	19.178	88.5216	Flooded depression	18	0.22	3	HCO3--Ca<<Na	Quartz
		MEX	42	Emiliano Zapata	EMI	19.197	88.4691	Flooded depression	23	2.52	5	HCO3--Ca<<Na	Quartz and phyllosilicates
		MEX	43	Noh-bec	NOH	19.146	88.1762	Flooded depression	1	8.5	2.5	Cl<<SO4--Ca--Mg	Nd
		MEX	44	Miguel Hidalgo	MIG	18.786	88.3674	Flooded depression	31	20.22	4	HCO3<<SO4--Ca<<Na	Calcite
		MEX	45	Misteriosa	MIS	18.042	90.4980	unknown	53	5	5.8	SO4<<Cl--Ca	Quartz
GSHN	GSHN1	SAL	46	Olomega	OLO	13.307	88.055	volcanic	66	25.2	2.5	HCO3--Na<<Mg	Phyllosilicates
		SAL	47	Apastepeque	APA	13.692	88.745	volcanic, crater lake	509	0.38	47	HCO3--Mg<<Ca	Feldspars
		SAL	48	Guija[b]	GUI	14.261	89.501	volcanic, lava flows	431	45	22	SO4<<Cl--Ca<<Na	Nd
		SAL	49	Jocotal	JOC	13.337	88.252	volcanic, lava flows	26	8.7	3	HCO3--Na--Mg	Feldspars and phyllosilicates
		SAL	50	Nagualapa	NAG	13.470	89.002	volcanic	43	0.12	1	HCO3--Na--Mg	Nd
		SAL	51	El espino	ESP	13.953	89.865	volcanic	689	0.99	5.5	HCO3<<SO4--Mg<<Na	Phyllosilicates
		SAL	52	Los negritos	NEG	13.283	87.937	volcanic	102	0.69	2	HCO3<<Cl--Na<<Mg	Phyllosilicates
		NIC	53	Masaya	MAS	11.996	86.116	volcano-tectonic	222	8.33	ND	HCO3--Na<<Mg	Feldspars
		NIC	54	Managua	MAN	12.270	86.477	volcano-tectonic	41	1061.17	ND	HCO3<<Cl--Na<<Mg	Feldspars
		SAL	55	Chanmico	CHA	13.779	89.354	volcanic, crater lake	477	0.78	51	HCO3<<SO4--Mg<<Na	Feldspars
		SAL	56	Aramuaca	ARA	13.429	88.107	volcanic, maar lake	76	0.4	107	SO4<<HCO3--Na<<Mg	Feldspars
		MEX	57	Tekom	TEK	20.73	89.4660	karst	24	<0.01	3	HCO3<<SO4--Ca<<Na	Calcite
		HON	58	Jucutuma	JUC	15.512	87.903	Flooded depression	27	4.34	2	HCO3--Ca<<Na	Quartz and phyllosilicates

		HON	59	Ticamaya	TIC	15.551	87.890	Flooded depression	17	2.91	2	HCO3<<Cl--Ca--Na	Nd
		HON	60	Yojoa	YOJ	14.861	87.985	volcanic	639	79.7	22	HCO3-Ca	Quartz
		SAL	61	Metapan	MET	14.309	89.466	volcanic	450	16	6	HCO3-Ca	Quartz
	GSHN2	SAL	62	Ilopango	ILO	13.682	89.071	volcanic, caldera lake	446	70.28	177	Cl<<HCO3--Na	Nd
		SAL	63	Coatepeque	COA	13.862	89.553	volcanic, caldera lake	743	26	119	Cl<<HCO3--Na<<Mg	Feldspars
		NIC	64	Nicaragua	NIC	11.460	85.774	volcano-tectonic	37	8264	ND	HCO3<<Cl--Na<<Ca	Nd
	GSHN3	GUA	65	Chicabal	CH1	14.788	91.656	volcanic, crater lake	2726	0.21	10.3	SO4--Mg	feldspars
		GUA	66	Calderas	CAL	14.412	90.591	volcanic, crater lake	1790	0.35	26	HCO3--Mg<<Ca	feldspars
		SAL	67	Verde	VER	13.891	89.787	volcanic, crater lake	1609	0.1	12	HCO3--Mg<<Ca	Feldspars
		GUA	68	San Juan Bautista	JUA	14.042	90.072	Flooded depression	1285	0.07	2	HCO3--Mg<<Ca	feldspars
		SAL	69	Alegria	ALE	13.493	88.493	volcanic, crater lake	1272	0.09	10	SO4--Ca<<Mg	Feldspars
		GUA	70	Atitlán	ATI	14.684	91.224	volcanic, caldera lake	1556	125	340	HCO3--Mg--Na	Nd
		GUA	71	Amatitlán	AMA	14.436	90.548	Volcanic	1193	15.2	23	HCO3--Cl--Na<<Mg	Calcite
		GUA	72	Magdalena	MAG	15.543	91.396	tectonic	2863	0.01	2.8	HCO3-Ca	Calcite
		HON	73	Madre vieja	MAD	14.357	88.138	Flooded depression	1866	0.1	3.4	HCO3--Mg<<Ca	phyllosilicates
		HON	74	Chiligatoro	CH2	14.376	88.183	volcanic	1925	0.04	5.5	SO4--Mg	Quartz
		GUA	75	El pino	PIN	14.345	90.394	volcanic	1038	0.64	6	HCO3--Mg<<Ca	phyllosilicates
		GUA	76	Ipala	IPA	14.557	89.639	volcanic, crater lake	1495	0.56	25	HCO3--Mg<<Na	feldspars

a= Maximum sampled water depth b= Pérez et al., 2011 Nd=not determined

For the YG region, the first PCA run identifies thirteen uncorrelated variables. The second PCA run clearly explains the variation of the data set (Fig. 3a). The first (PC1) and second (PC2) components explain 38% of the total variance of the data set (Fig. 3a, Table S2.1). The PC1 accounts for 23.4%, and the PC2 for 14.6% of the total variance, respectively. The biplot based on component 1 and 2 indicates that conductivity (ranging from 175 to 3479 µS cm^{-1}) and related ions sodium (Na^{+}), chloride (Cl) and magnesium (Mg^{2+}) are the variables that exhibit the highest correlations (<0.64) with the first principal component Fig. 3a-c). Thus, they represent the most influential variables differentiating aquatic ecosystems in the YG region. pH, ranging from 6.9 to 9.9, was highly correlated (>0.73) with the second component (PC2), suggesting that it is the second most influential variable of the YG aquatic environments (Fig. 3a, d, Table S2.1). Figures 3 b, c and d show regional distribution of the most meaningful variables for the YG region.

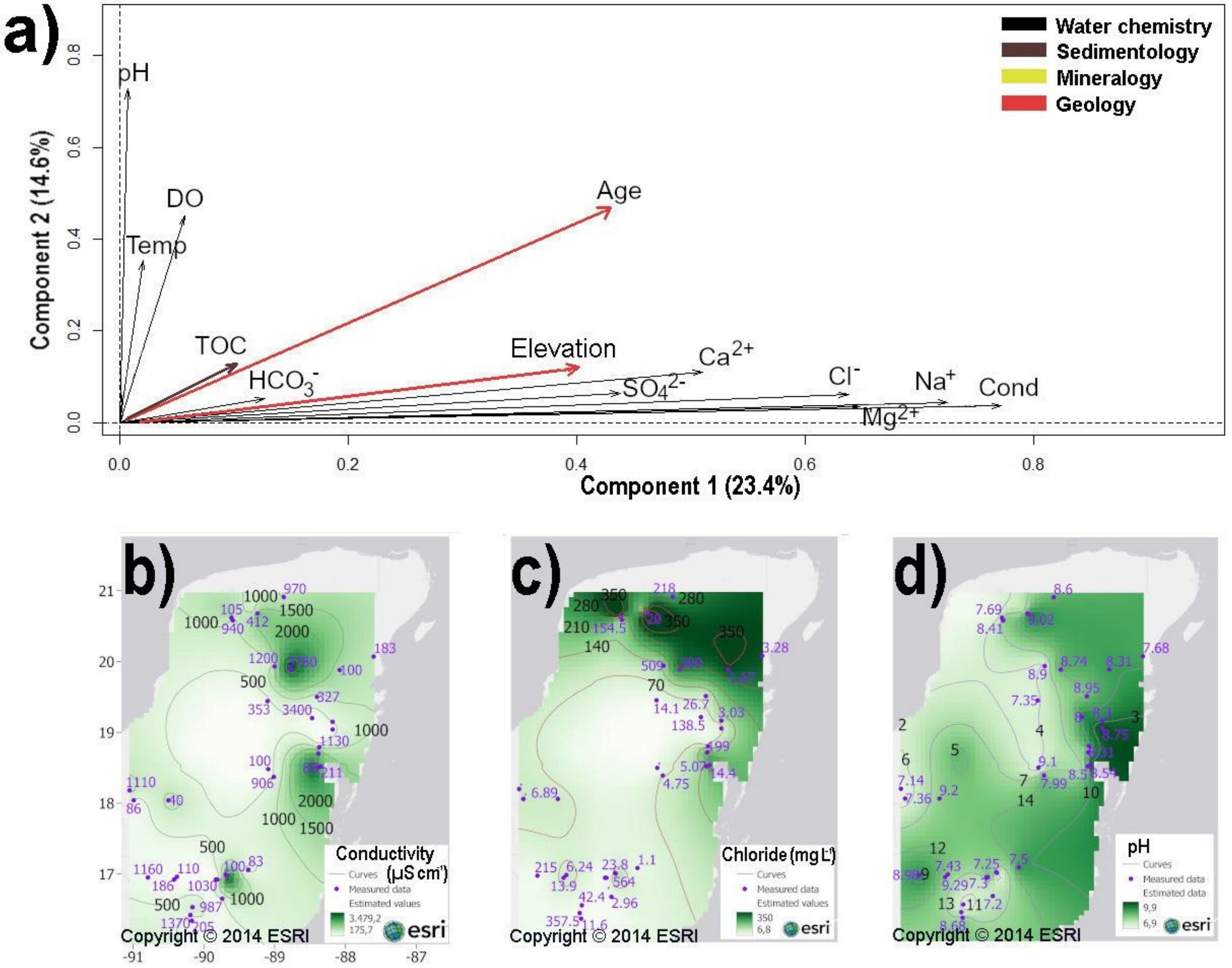

Figure 3 (a) PCA biplot based on 13 variables from 45 aquatic ecosystems of the Yucatán Peninsula and northern Guatemala (YG limnological region). Conductivity and related ions were the most meaningful variables characterizing aquatic ecosystems as they explain 23.4% of the total variance. The second most important variable is pH, accounting for 14.6% of the total variance. Arrows represent variables. Spatial representations of meaningful variables are presented in (b-d) interpolated maps of conductivity (b); chloride (c); pH (d). Abbreviations are as follows: temperature (temp) (ºC), conductivity (cond) (µS cm^{-1}), magnesium (Mg^{2+}), chloride (Cl^{-}), bicarbonate (HCO_3^{-}), potassium (K^{+}), calcium (Ca^{2+}), sodium (Na^{+}), sulfates (SO_4^{2-}) dissolved oxygen (DO) (µmol L^{-1}) and total organic carbon (TOC). Major ions concentrations are expressed in mg L^{-1}. Blue numbers in maps represent measured values, black numbers are interpolated values.

For the GSHN region, the PCA based on 13 uncorrelated variables, explains 49.6% of the total variance of the data set, within the first (PC1) and second (PC2) components (Fig. 4a, Table S2.2). PC1 accounts for 26.8% and PC2 for the 22.8% of the total variance. The PCA biplot based on components 1 and 2, respectively, shows that water ionic composition, particularly content of bicarbonates (HCO_3, ranging from 4 to 373 mg L^{-1}), sodium (Na^+, ranging from 2 to 180 mg L^{-1}) and chloride, is the most influential in discriminating aquatic systems in the GSHN region, as it correlated >0.62 with the first component (Fig. 4a-c, Table S2.2). Geochemical and geological variables such as TOC (ranging from 5 to 22.9%), age and bedrock are the second most influential variables as they are strongly correlated with the second component (> 0.75) (Fig. 4a, d). Figure 4 b, c, d show the spatial distribution of meaningful variables for the GSHN region.

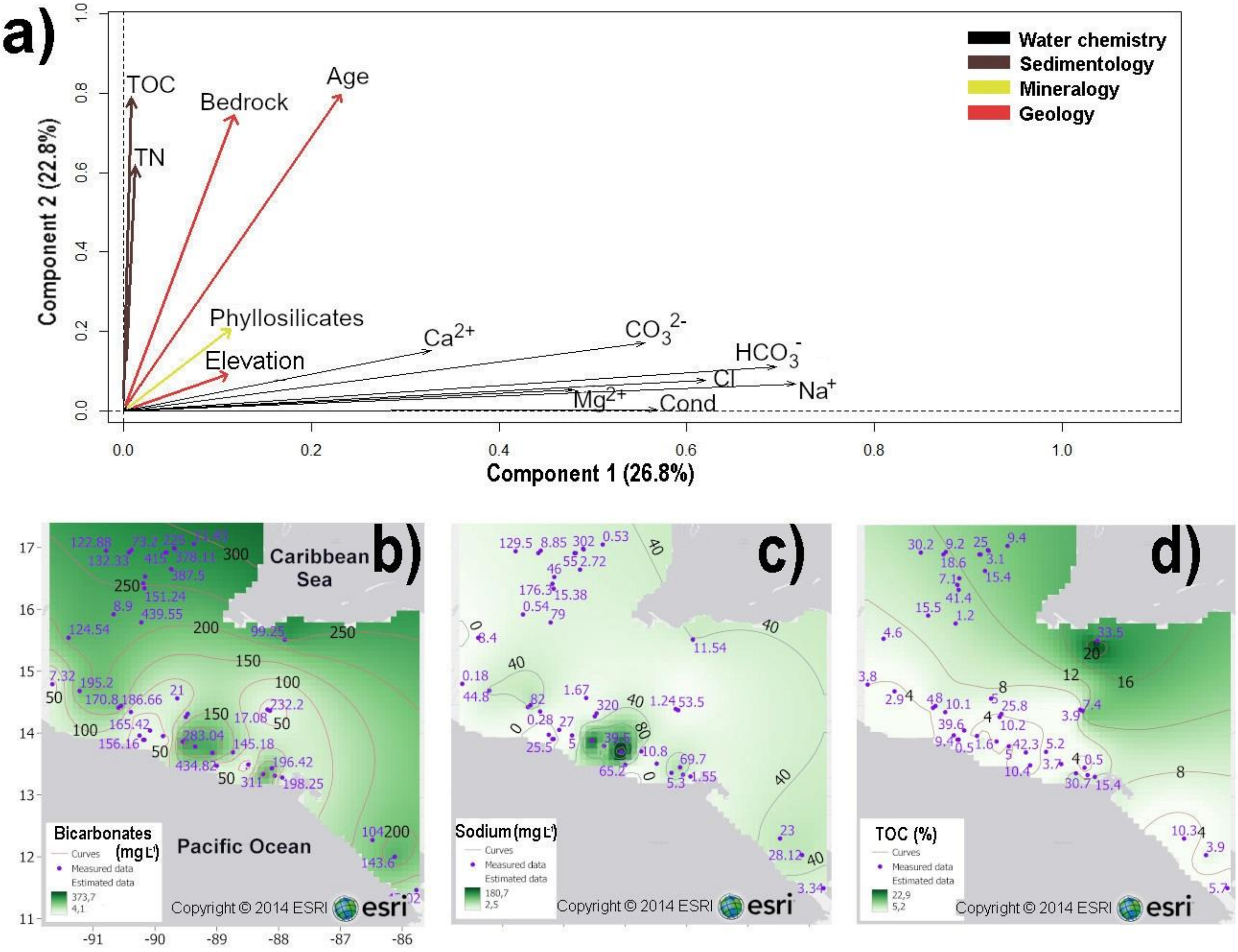

Figure 4 (a) PCA biplot based on 13 variables from 31 aquatic ecosystems of central-southern Guatemala, El Salvador, Honduras and Nicaragua (GSHN limnological region). Ionic composition HCO_3^-, Na^+, Cl^- were the most meaningful variables characterizing aquatic ecosystems, as they explain 26.8% of the total variance. Sediment geochemistry and geology were the second most important variables, accounting for 22.8% of the total variance. Arrows represent variables. Spatial representations of meaningful variables are presented in (b-d) interpolated maps of bicarbonates (b); sodium (c); TOC (d). Abbreviations are as follows: conductivity (cond) (µS cm^{-1}), magnesium (Mg^{2+}), sodium (Na^+), chloride (Cl^-), bicarbonate (HCO_3^-), carbonates (CO_3^{2-}), calcium (Ca^{2+}), total nitrogen (TN) and total organic carbon (TOC). Major ion concentrations are expressed in mg L^{-1}. Blue numbers in maps represent measured values, black numbers are interpolated values.

Water ionic dominance was graphically evaluated with ternary plots (Fig. S1 and Fig. S2) and information on lake water types is shown in Table 1. Here, we highlight the most relevant characteristics for YG and GSHN limnological subregions:

3.2 The YG region composed by karst aquatic systems

In the YG limnological region, four subregions were identified in the cluster analysis. The first subregion (YG1; n=9) within YG included systems located in central-southern Yucatán and in the northern Petén district in Guatemala (Fig. 2). Lakes are located in the lowlands (<170 m a.s.l.) and most of them are relatively shallow (<16 m depth), such as Bacalar, Encantada, Sabana Chetumal, Rosario, Salpetén, Chichancanab, except for Lake Petexbatún (40 m depth) and Lachuá (378 m depth). The latter constitutes the deepest lake in the study area. Waters of these systems are dominated primarily by sulfates, followed by calcium and magnesium. The YG limnological subregion YG2 (n=15) contains lakes that are mostly restricted to the Guatemalan lowlands (Fig. 2). Most of these systems are large lakes, including Lake Petén Itzá, one of the largest (100 km^2), deepest (165 m) and oldest (~400 ka) lakes of the northern Neotropics. Lake waters are dominated by carbonates, and therefore calcium prevails in these lakes. Aquatic systems located in the central and northern portion of the Yucatán Peninsula were grouped in YG3 (n=11) (Fig. 2). Colac, Sabak ha, Mucuyche, Oxolá, Gruta Miguel Hidalgo and Yumku are *cenotes* in northern Yucatán, and lakes Yalahau, Caobas, Kaná, Señor and Muyil are located in the central-northern Peninsula. Carbonates dominate lake waters and chloride shows high values. Limnological subregion YG4 (n=10) consists of lakes located in the central-southern Yucatán Peninsula (Fig. 2). Lakes are relatively large, shallow and far from the Caribbean and Gulf of Mexico coasts, at least >60 km, e.g., Silvituc and Chacanbacab. Waters are dominated by carbonates and calcium.

Mineralogical analysis reveals that most lakes are dominated by carbonates in the YG limnological region. In subregions YG1 and YG3 (central and northern Yucatán Peninsula), most lake sediments have calcite as the dominant mineral (Table 1, Fig. S2). Lakes Chichancanab and Salpetén both belong to YG, but show carbonates with a co-dominance of phyllosilicates and gypsum. Lakes from YG2 are mainly dominated by phyllosilicates and feldspars. The mineralogical composition of lake sediments of the YG4 subgroup varies. Sediments of the lakes such as Vallehermoso, Emiliano Zapata and Chacanbacab are dominated by phyllosilicates with or without feldspars. Sediments of lakes such as Miguel Hidalgo, on the other hand, are dominated by carbonates, with calcite as main mineral, whereas Lake Silvituc is characterized by exotic minerals such as silver and gold (Table S1).

3.3 The GSHN limnological region is composed by volcanic aquatic systems

In the GSHN region, three subregions were identified by cluster analysis. Lakes of GSHN1 (n=16) are located in Central America at low and middle elevations, ranging from 17 to 689 m a.s.l. Lake waters show a clear dominance of carbonates, followed by sodium, potassium and magnesium (Table 1, Fig. S3). The GSHN2 is composed of three of the largest lakes in Central America: Ilopango, Coatepeque and Nicaragua. These three lakes originated from volcanic activity. Lakes Ilopango and Coatepeque are caldera lakes, whereas Lake Nicaragua surrounds Volcanoes Concepción and Maderas. There is no clear pattern for ions in the water column, but sodium and potassium dominated, followed by magnesium. The GSHN3 (n= 12) is formed mainly by crater lakes located in the highlands of Guatemala, Honduras and El Salvador. Most lake waters are dominated by bicarbonates, followed by magnesium, whereas Chiligatoro, Chicabal and Alegría are dominated by sulfates (Table 1, Fig. S3).

Sediment mineralogy of Central American lakes (GSHN region) shows that most subgroups are dominated by feldspars. Co-dominance with other minerals such as phyllosilicates and carbonates occurs. The GSHN1 combines lakes dominated by phyllosilicates and feldspars, whereas quartz is the dominant mineral in Lakes Yojoa and Ticamaya (Honduras). GSHN2 includes large lakes dominated by feldspars. In Lake Nicaragua, this dominance is also shared with phyllosilicates. For the GSHN3, we detected two main mineral assemblages. The first is dominated by phyllosilicates and feldspars, with clay minerals and feldspars as main minerals, and the second is dominated by feldspars and phyllosilicates.

3.4 Ostracode species associations and their relationship with limnological regions

We found ostracode species in 74 of the 76 of the aquatic systems we studied in the northern Neotropics. In the volcanic Lake Alegría (El Salvador) and the karstic cave San Miguel (Yucatán, Mexico), ostracodes were not observed. Living adult specimens were encountered in samples from all systems, except those from Lakes Chicabal, Tekoh, Yaxhá, Verde and Cenote Mucuyche, where only empty shells or single valves were recovered. Taxonomic analysis of species enabled us to identify 70 species (Table S3), out of which 31 were recorded at single sites, whereas the remaining 39 were observed in at least two systems. Species richness ranged between 1 to 9 with an average of 4 species per site, whereas the Shannon Diversity Index (H) maximum value was 2.1, corresponding to Lakes Bacalar and Petén Itzá and the Candelaria River. For all other lakes the index averaged 1.1. The list of ostracode species found in our study is presented in Table S3.

NMDS ordination, based on species occurrence data, revealed five major species associations (OST 1-5) with a reliable stress value of 0.08 (Fig. 5a) (Clarke, 1993). The PERMANOVA test shows statistically significant differences between group centroids ($F = 1.19$, $p = 0.0001$), thus supporting NMDS ordinations. Ostracode groups 1 and 2 are located in the YG limnological region (karst terraces), and groups 3-5 in the limnological region GSHN (volcanic Guatemalan highlands and Central American mid-elevations and lowlands). The first species group (OST1) consists of twelve ostracode species, recorded from lakes and *cenotes* from the eastern Yucatán Peninsula (Fig. 5b). Most of these species are tolerant of high conductivity (particularly related to Na^+ and Cl^-), such as *Heterocypris punctata* and *Limnocythere floridensis* (Fig. 5c) *Cyprideis* cf.

salebrosa and *Perissocytheridea* cf. *cribrosa*. The second species group (OST 2) includes 11 species, distributed in lakes and ponds of the southern Yucatán Peninsula and northern Guatemala (Fig. 5b). Some of these species (Fig. 5b), such as *Cypria petenensis*, *Cypretta campechensis* and *Paracythereis opesta*, are considered endemic (Cohuo et al., 2016). Some others, such as *Alicenula serricaudata*, *Pseudocandona antilliana* and *Cytheridella ilosvayi*, have a wide Neotropical distribution (Cohuo et al., 2016). The third species group (OST 3) consists of seven species distributed mainly in mid-elevation lakes from Guatemala, El Salvador, and Honduras (Fig. 5b). Several of these species have very restricted distributions and correspond to the *Strandesia*, *Keysercypria* and *Cypridopsis* genera (Fig. 5c). The fourth species group (OST 4) is composed of six species: *Heterocypris nicaraguensis*, *Potamocypris islagrandensis*, *Cypria granadae*, *Limnocytherina royi*, *Perissocythere marginata* and *Cyprideis* sp., distributed exclusively in lakes in Nicaragua (Figs. 5a, b). The fifth group (OST 5) includes only three species from highland lakes of Guatemala: *Chlamydotheca* cf. *colombiensis*, *Cypria* sp. 4 and *Cypridopsis* sp. 7 (Figs. 5b, c).

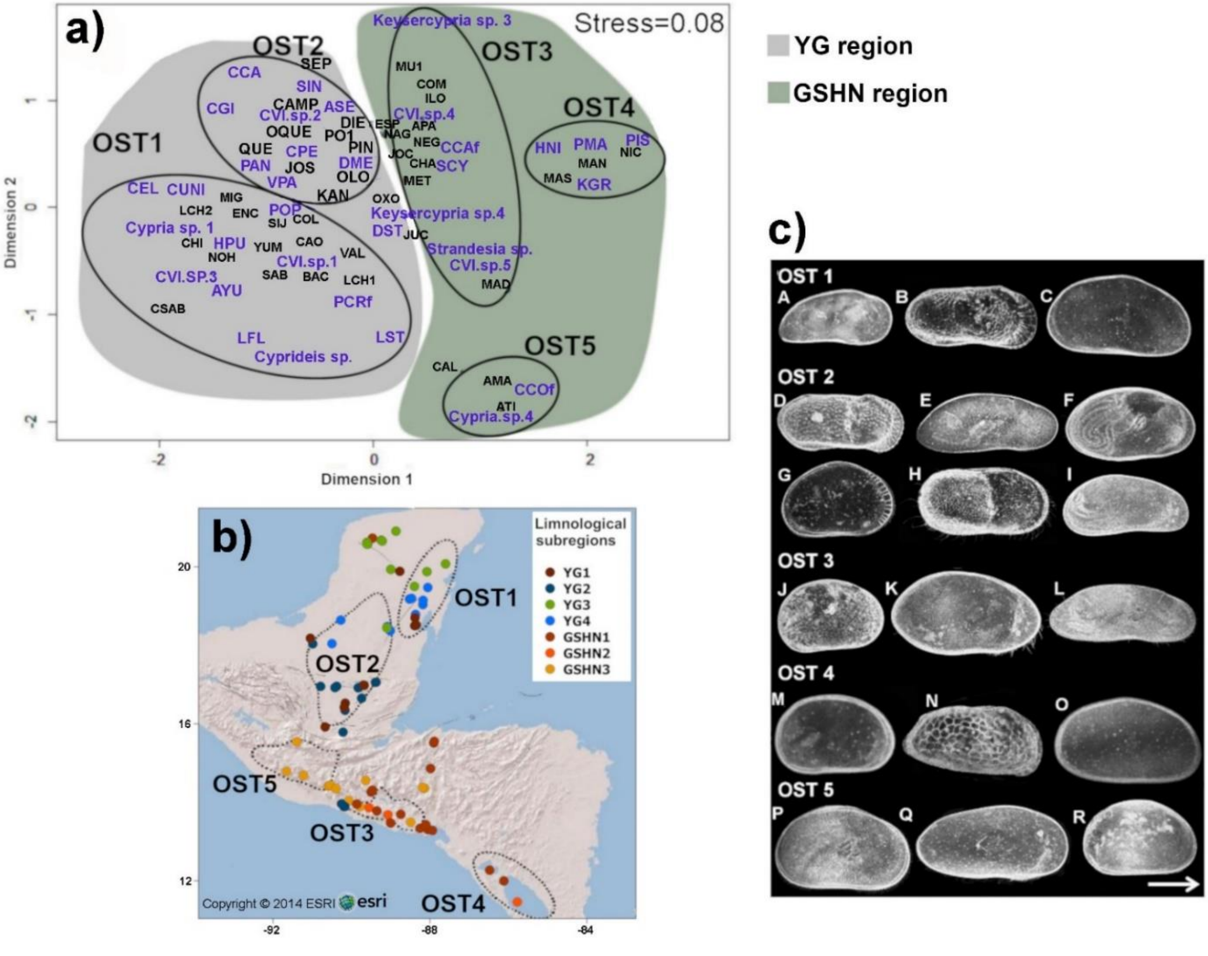

Figure 5 (a) Non-metric multidimensional scaling (NMDS) plot showing differences in ostracode species composition among the 76 studied aquatic ecosystems. Results are based on the Bray-Curtis dissimilarity index, using species presence/absence data (stress = 0.08). Black lines indicate ostracode group associations (OST 1, 2, 3, 4, 5). For species name abbreviations see Table S3. (b) map showing spatial distribution of species associations. (c) Plate of selected freshwater ostracode species of each limnological subregion of the northern Neotropical region. A) *Thalassocypria* sp.; B) *Limnocythere floridensis*; C) *Heterocypris punctata*; D) *Paracythereis opesta*; E) *Diaphanocypris meridana*; F) *Strandesia intrepida*; G) *Cypretta maya*; H) *Cytheridella ilosvayi*; I) *Pseudocandona antilliana*; J) *Keysercypria* sp. 4; K) *Strandesia* sp.; L) *Stenocypris cylindrical major* M) *Cypria granadae*; N) *Perissocytheridea* cf. *cribrosa*; O) *Heterocypris nicaraguensis*; P) *Hemicypris* sp.; Q) *Pseudostrandesia* sp.; R) *Cypria* sp. 4.

3.4.1 Relating ostracode distributions to environmental variables

Results of the DCA analysis revealed gradient lengths of 8.2 and 4.9 SD units for first and second axis, respectively. Thus, a canonical correspondence analysis (CCA) was used to assess the relationship between species and environment (Šmilauer and Lepš, 2014). Using the forward selection technique, we found a set of eight variables that best explain the variance of data (Table S4.1). The first two axes of the CCA account for 47.4% of the variance of the species-environment relationship and 13.1% of the variance of species data. The summary of performance and ordination of this analysis are presented in Table S4.2. The first axis of the CCA plot (Fig. S3) explains 25.8% of the correlation between species and explanatory variables, with a canonical coefficient of 0.95 and an eigenvalue of 0.81. Sedimentary bedrock, TOC, temperature, and feldspars are the most important factors that influenced species composition on axis 1 (Fig. S3). Axis 2 is strongly correlated with plutonic bedrock, elevation, and phyllosilicates. This axis explains 21.6% of the species-environment relationship, with a canonical coefficient of 0.90 and an eigenvalue of 0.68. In the CCA ordination, OST1 is positively correlated with conductivity and bedrock of sedimentary origin. OST 3 and OST 4 are positively correlated to volcanic and plutonic bedrock. OST 5 is associated with sediments dominated by feldspars. OST2 is positioned close to the center of the axes, suggesting that species are broadly tolerant of the variables analyzed.

3.5 Structural equation modelling

Five models of the relationships of geodiversity, limnology and species composition and richness were tested with structural equation modelling (SEM). Four models used geodiversity only as exogenous variables (models 1-2, 4-5), and in one model (model 3) limnology was also considered as an exogenous variable (two exogenous variables, explaining an endogenous variable). Description of the rationale behind variable selection and relationships tested in each model are found in section S1 of the Supplementary Material. Model 1 evaluated the direct influence of geodiversity on limnology and the influence of limnology on species composition, resulting in the following metrics of global fit: CFI 0.63, RMSEA 0.19, and SRMR 0.12. Model 2, tested relationships similar to model 1, but additionally the relevance of TOC on species composition and richness, with the following statistics: CFI 0.79, RMSEA 0.13, and SRMR 0.14. Models 1 and 2 received relatively low values of global fit, all below the threshold of statistical significance. Values of a Chi-square test were < 0.05 in these two models, and they were therefore rejected as explanatory models.

Model 3 evaluated the influence of two exogenous variables, geodiversity and limnology, on species composition. Geodiversity and limnology were considered independent and without any influence on one another. Metrics of global fit of this model were better than in models 1 and 2, (CFI 0.94, RMSEA 0.06, and SRMR 0.14). However, the data were too small to calculate the statistical significance of both exogenous variables, and then, interpretation of the results is not reliable. This model was also rejected.

Model 4 and model 5 evaluated the same relationships between geodiversity, limnology and species composition and richness as in model 1, but additionally, the individual influence of elevation and conductivity (model 4) and TOC and latitude (model 5) were analyzed. Model 5 received the following metrics of global fit CFI 0.62, RMSEA 0.20, and SRMR 0.17, all below the threshold of significance, and the model was therefore rejected. The optimal model was model 4 (Fig. 6). This is supported by the following metrics of global fit, CFI = 0.93 (values close to 1 indicate better fit of the model), RMSEA = 0.01 (values < 0.05 are considered reliable; Fabrigar et al., 1999) and SRMR=0.03 (values < 0.08 are generally considered a good fit; Hu and Bentler, 1999). The optimal model suggests that geodiversity strongly influences limnology. Limnology explains species composition (distribution), but not species richness. Elevation and conductivity do not explain species richness but demonstrate significant influences on species composition. The direct influence of limnology on species composition was statistically significant, whereas it did not exert an influence on species richness (p-value > 0.05).

All paths in figure 6 are statistically significant (p-value <0.05), except for the direct effect of limnology, conductivity, and elevation on species richness.

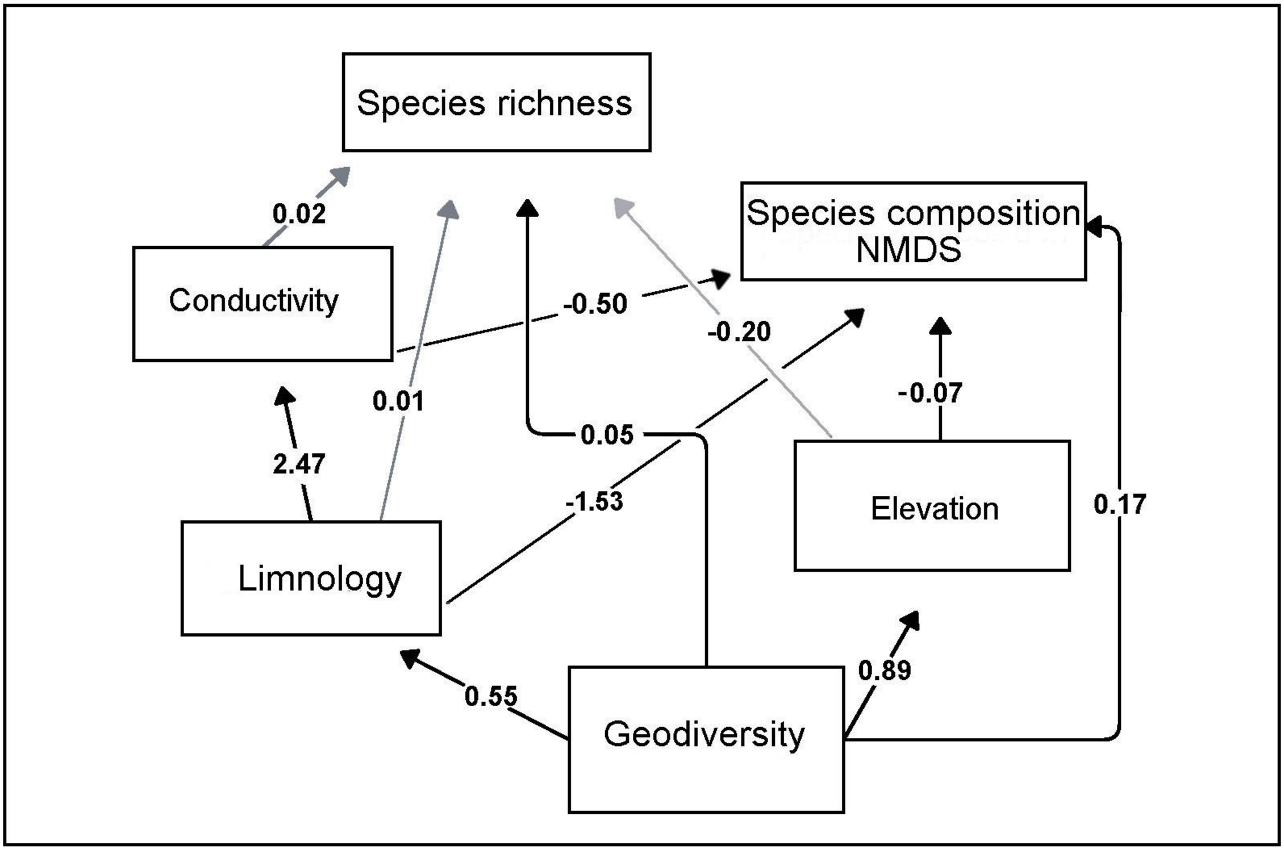

Figure 6. Structural equation modelling of the influence of geodiversity and related variables with freshwater ostracode species composition and distribution. Metrics of global fit of the optimal model CFI = 0.961, RMSEA = 0.01, and SRMR=0.036. Arrows indicate the direction of influence. Black arrows are paths statistically significant at p-value <0.05, and gray paths are not significant. Numbers next to arrows are the path standardized coefficients.

4. Discussion

4.1 Geodiversity drives two main limnological regions in the northern Neotropics

Our cluster analysis based on 76 lakes and 23 lake attributes shows limnological regionalization in the northern Neotropics. Two main regions, corresponding to Yucatán Peninsula-northern Guatemala (Group YG) and northern Central America (Group GSHN), were identified (Fig. 2). The group YG is located in karstic plateaus of sedimentary origin, dominated by limestone, dolomite, evaporites and carbonate-rich impact breccia (Hildebrand et al., 1995; Schmitter-Soto et al., 2002a, b; Vázquez-Domínguez and Arita, 2010). The Group GSHN is located in volcanic bedrock terrains of Guatemala, El Salvador, Honduras and Nicaragua, where pyroclastic and volcanic epiclastic materials, usually reworked, are abundant, reflecting active or past volcanic activity (Dengo et al., 1970; Stoiber and Carr, 1973; Carr, 1984). The YG and the GSHN groups were further subdivided into four (YG1-4) and three subgroups (GSHN1-3), representing limnological subregions. This proposed regionalization, therefore, reveals high heterogeneity of aquatic systems in the northern Neotropics. Multivariate statistics (PCA) shows that regions and subregions can be distinguished by ionic composition of waters. Geochemical variables related to sediments, such as TOC and mineral composition, are recognized as the second most important characteristics (Figs. 3, 4).

In the YG karst region, lakes are characterized by carbonate-, calcium- and calcite-signatures, which is expected because waters interact with limestone and dolomite-rich bedrock on the Peninsula (Schmitter-Soto et al., 2002a, b; Perry et al., 2009). This is also responsible for the dominance of calcium, sodium, and magnesium ions in waters, which in turn are related to the generally alkaline surface waters in most aquatic systems of the region (Alcocer et al., 1998; Schmitter-Soto et al., 2002a, b) (Figs. 3a, d). In specific areas, such as YG3, dominance of chloride is also relevant. This can be explained by two main processes, 1) marine intrusion and 2) input of subterranean waters that have interacted with evaporites. The spatial distribution map of chloride contents in lake waters (Fig. 3c) shows a clear tendency to higher values on the northern Yucatán Peninsula where marine intrusion is probably the most important source of chloride (Sánchez-Sánchez et al., 2015; Saint-Loup et al., 2018). Marine intrusions in northern Yucatán have been mapped as far as 100 km inland (Steinich and Marín, 1996). Pérez-Ceballos et al. (2012) found that several water systems, mainly *cenotes*, in this same region are characterized by marine waters below freshwater lenses, with water intermixing.

Sulfate is an interesting component of some lakes of the YG1 systems (Socki et al., 2002; Pérez-Ceballos et al., 2012). The presence of sulfates in lake waters may be attributed to the K/T anhydrite/gypsum–bearing impact breccia and dissolution of $CaSO_4$ of evaporites (Rosencrantz, 1990). This suggests that lakes with high sulfate contents receive high ground water input, as evaporites are only present at depths greater than 170 m below surface, or that these lakes developed along sites with past tectonic activity such as faulting and uplift (Perry et al., 2002). Some lakes from the YG1 with high content of sulfates did, in fact, develop along fault zones. For example, Lake Chichancanab is associated with the Sierrita de Ticul fault (Hodell et al., 2005) and Lachuá to the Polochic fault (Erdlac and Anderson, 1982), whereas other lakes are related to high ground water input, such as the Bacalar hydrological system (Perry et al., 2009).

High TOC values in sediments of most lakes of YG2 probably reflect the trophic state of lake waters. Our data confirm results by Pérez et al. (2011a), who recorded a TOC increase from north to south on the Yucatán Peninsula. This may be attributed to the combined effect of soil, precipitation and vegetation type, which changes from north to south. The northern part of the Yucatán Peninsula is characterized by leptosols, which are shallow soils with high amounts of exposed hard rock and calcareous material (Bautista et al., 2011; Estrada-Medina et al., 2013). There, precipitation of about 450 mm yr^{-1} (Pérez et al., 2011a), gives rise to low-stature deciduous forests with low biological productivity. In the south of the peninsula, where precipitation increases to >3200 mm yr^{-1} (Pérez et al., 2011a), luvisols and vertisols, clayey and fertile soils, support the growth of tropical evergreen forests that generate high amounts of organic matter runoff, particularly during the rainy season.

Most Central American lakes owe their origin to volcanism. These lakes are classified as caldera lakes, crater lakes in (partially) active or inactive volcanoes, maar lakes, or are located in volcanic bedrock basins (Golombek and Carr, 1978; Newhall and Dzurisin, 1988; Dull et al., 2001; Vallance and Calvert, 2003) (Table 1). The existence of at least three limnological subregions highlights that these lakes are additionally influenced by regional factors related to orography (elevation), climate and the level of volcanic activity, including magmatic heat and gas input. Ionic dominance of Central American lakes is highly variable, but anions Cl^-, SO_4^{2-}, and cations K^+, Mg^{2+}, Na^+ were dominant (Fig. 4a). This ionic composition reveals that two main processes control water chemistry: 1) active volcanic activity with strong interaction with lakes, and 2) precipitation-evaporation rates, especially at high-elevation sites. Dominance of magnesium, chloride and sulfates, such as in GSHN3, can be attributed to volcanic activity and hydrothermal systems. Chloride and sulfates are strongly influenced by volcanic gas input, by incorporation of HCl and SO_2, and interaction with igneous rocks. Lakes with such ionic dominance also display high contents of phyllosilicates and feldspars, which may have formed through dissolution by hot and likely acid groundwater, heated by hydrothermal activity. Lakes located in the Transmexican Volcanic Belt of central Mexico (TMVB; Armienta et al., 2008; Sigala, et al., 2017) have similar ionic and sediment chemical composition as lakes in Central America. The ionic dominance of the currently extinct crater lakes of Volcano Popocatepetl, for example, changed from sulfate to calcium-magnesium dominance and finally magnesium dominance, resulting from heating of andesite rocks after a period of increased volcanic activity (Armienta et al., 2000, 2008). This suggests that the influence of active volcanism on lake water chemistry may exert similar influences along the northern Neotropical region and American transition zone. High rates of evaporation are anticipated to represent an important driver for water chemistry in Central America as well, because of dominance of carbonates, bicarbonates and sodium (GSHN1 subregion). This ionic composition can be attributed to interaction and weathering of volcanic rocks, capture and dissolution of $CO_{2,}$ and high evaporation rates. Although Central America can be considered a tropical and humid region, high temperatures and solar radiation, especially at high elevations, may produce high evaporation rates leading to ion- specific signatures such as dominance of carbonates-bicarbonates.

Given the origin of discriminating variables in PCA for both YG and GSHN, we found three main sources controlling limnology in the northern Neotropics: (i) bedrock type, which determines specific mineral and ionic composition of lake sediments and host waters; (ii) volcanic and marine influence, which determines the presence of dominant and conservative ions such as Mg^{2+} and Cl^- , and (iii) precipitation-evaporation balance across altitudinal and latitudinal gradients, which determines the concentration of solutes and therefore conductivity. This is consistent with results from limnological studies in other regions of Central America and southern Mexico, which suggested that geology, through bedrock types and volcanic input to lakes, and marine interactions, are the most influential factors for aquatic environments (Löffler,1972; Haberyan and Horn, 1999; Haberyan et al., 2003; Cervantes-Martínez et al., 2002; Perry et al., 2002; Schmitter-Soto et al., 2002a; Socki et al., 2002; Pérez et al., 2011a). Several authors, however, consider additional features relevant for lake classification, such as temperature, pH and altitude (orography) (Brezonik and Fox, 1974; Horn and Haberyan, 1993; Umaña et al., 1999; Haberyan et al., 2003). In our study, water temperature, pH and elevation scored relatively low on the PCA, suggesting that their influence is relevant only on a local scale. Considering the determinants of limnological variability of aquatic systems at both regional and local scales, the interaction with marine environments and the high variability of aquatic system morphology and origin, it is evident that the current geological configuration is the main factor driving aquatic ecosystem properties and defining limnological regions in the northern Neotropics.

4.2 Geodiversity as a determinant of distribution of freshwater ostracodes in the northern Neotropics

We found ostracode species in almost all the aquatic systems we studied. Seventy species were recognized, demonstrating that this group is abundant and diverse in the northern Neotropics. The number of species per lake (species richness), however, was relatively low. In most sites we found between two and six species, and in large lakes, such as Petén Itzá and Nicaragua, we found a maximum of nine species. Diversity metrics substantiated this tendency, with values of the Shannon Index always < 2, which reflects low diversity in aquatic environments (Margalef, 1957; Chao and Shen, 2003). Low species richness was also observed in previous studies in the region. In Lake Petén Itzá, for example, a maximum of 11 species was reported by Pérez et al., (2010a). In Lake Nicaragua, the largest lake in Central America, seven species were found (Hartmann, 1959). In contrast, in regions such as the Palearctic, a single lake may host 32 species, such as ancient Lake Ohrid (Macedonia/Albania), although there, the Shannon Diversity Index revealed low diversity (H=1.2) (Lorenschat et al., 2014), whereas small lakes in Europe, such as Lake Maarsseveen may harbor 9 to 15 species (Sluys, 1981). In Japan, 40 species were recorded from Lake Biwa (Karanovic, 2015). This global species richness pattern contrasts with the Latitudinal Diversity Gradient theory, that postulates an increase in species richness from the poles to the Equator (Mannion et al., 2014; Schumm et al., 2019). Nevertheless, a similar pattern, i.e. a decline in diversity at lower latitudes is observed for other aquatic microorganisms in the northern Neotropics, such as testate amoebae (Sigala et al., 2016; Sigala Regalado et al., 2018; Charqueño-Celis et al., 2019), chironomids (Hamerlík et al., 2018), and cladocerans (Vázquez-Molina et al., 2016; Wojewódka et al., 2016). Low species richness in lakes of the northern Neotropics may be related to local environmental and evolutionary processes that occurred in recent geologic time, namely during the Pleistocene and Holocene. For instance, in southern Mexico and northern Guatemala, severe droughts were inferred from study of sediment cores from Lake Petén Itzá (Mueller et al., 2010; Cohuo et al., 2018). Some of the droughts, such as those that occurred during Heinrich Stadials, probably caused most shallow lakes to desiccate (Cohuo et al., 2018). Repetitive droughts in the Pleistocene, with their consequent effect on surficial freshwater availability, must have impacted the biological evolutionary processes of ostracodes, which occupy benthic habitats, thus limiting species diversification and adaptation. An alternative explanation for the low ostracode species richness in the northern Neotropics is related to intensification of human activities in lakes and their watersheds. In Central America, water extraction, fisheries and fish farms, eutrophication and wastewater disposal, are among the most frequent alterations in freshwater ecosystem (Cuadra et al., 2006; Arcega-Cabrera et al., 2014; Campuzano et al., 2014). These conditions are known to strongly affect aquatic taxa, and particularly endemic species, sometimes causing loss of biodiversity (Moyle and Leidy, 1992). In the Neotropics, loss of both genetic and phenotypic biodiversity of aquatic taxa has been poorly evaluated (Johann et al., 2019), but is certainly an important issue that must be considered for lake protection and management (Mercado-Salas et al., 2013).

By comparison, in the flood plains of the Upper Parana River, South America, species richness can be as high as 44 (Higuti et al., 2017), which is higher than in lakes of Central America, and comparable to richness of lakes in temperate regions. In Colombian aquatic systems, however, such as La Fé reservoir (Saldarriaga and Martínez, 2010) and the Magdalena River basin (Roessler, 1990a, b), the number of ostracode species is similar to that in Central America (~6 species per lake). Therefore, to clarify structural patterns of ostracodes in the Neotropical region, more intensive sampling in lakes and rivers is needed. Evidence from other tropical regions around the world will be valuable to understand patterns of ostracode diversity (tropical vs temperate) and how latitudinal diversity gradients act in the Ostracoda group.

The NMDS analysis shows the existence of at least five species associations in the region (OST1-OST5), emphasizing that ostracodes do not conform to a faunal unit, but rather display disjunct faunas (Fig. 5a), similar to what is observed in freshwater fishes of the region (Miller, 1976; Matamoros et al., 2015). Ostracode associations are geographically delimited, and no overlap was observed (Fig. 5b). Ostracode groups OST1 and OST2, belong to the YG limnological region, whereas the OST3, OST4 and OST5 associations belong to the GHSN limnological region (Figs. 5a, b). Few species were present in more than three limnological subregions, and these can be considered of wide neotropical distribution, e.g., *C. ilosvayi* and *C. vidua*.

Correspondence between species associations and limnological subregions suggests a major influence of physical and chemical properties of lake environments on biological systems. The structural equation modelling (SEM) analysis exposed the significant influence of geodiversity on limnology, and of limnology on species associations, identified in the NMDS. This illustrates that limnology, particularly geochemistry, mineralogy, and water chemistry, is the primary factor responsible for species distributions in the study area. We were, however, unable to find statistical significance to explain the relationships between geodiversity and limnology with ostracode species richness. This suggest that the number of species per lake may not be fully governed by our predictors. For instance, conductivity and elevation in model 4 and TOC and latitude in model 5, also failed to explain species richness. This suggests that the main environmental gradients in the northern Neotropics, and the theorized increase in the number of species at lower latitudes (Latitudinal Diversity Gradient theory), do not apply in the northern Neotropics and, therefore, other intrinsic or extrinsic factors such historical water level fluctuations and precipitation/evaporation balance, might instead control species richness. In our SEM models, we also tested the direct influence of geodiversity and its indirect influence through limnology on species distribution and richness. The optimal SEM model demonstrated the significance of paths describing the direct influence of geodiversity on species richness and composition, but associated values were insignificant (<0.1). Conversely, strong ties were discovered when we analyzed for the indirect effect of geodiversity (via limnology) on species composition (>2.0). This implies that ostracode species composition is more predictable from limnological variables such as water physical and chemical and geochemistry than from geodiversity variables such as bedrock and mineralogy. Our SEM model also revealed that elevation is an important predictor of species composition (Fig. 6). The negative correlation suggested that an increase in elevation causes a decrease in the number of species per site. Most highland lakes were characterized by up to three species and, more commonly, by a single species, except for large lakes Amatitlán and Atitlán in Guatemala.

The CCA further demonstrates that geological components of the landscape such as bedrock, elevation (temperature), minerology and ionic composition are important for species distribution (Fig. S3). For instance, the OST1 group is represented by lakes of the YG3 subregion, associated with the Caribbean Sea coast (Fig. 5b). Similarly, the OST 2 group corresponds to lakes of the YG1 and YG2 subregions. These lakes are characterized by high TOC and abundant submerged vegetation. In Central America, patterns of coincidence between ostracodes and lake regions are evident, as well (Fig. 5b). The OST 4 and OST 5 groups are associated with volcanic-influenced lakes in the lowlands (GSHN1) and highlands (GSHN3), respectively. The CCA and SEM analyses show that the influence of geodiversity over species composition and distribution is only relevant when limnological attributes are taken into account. Future biogeographic studies should focus on combining different zooplankton and zoobenthos groups and explore the role of geodiversity in driving patterns of composition and distribution.

5 Conclusions

The northern Neotropics is a region characterized by high geodiversity, abundant aquatic systems, and high biodiversity. Our limnological survey of 76 aquatic environments identified two main limnological regions in the northern Neotropics. The YG region is associated with karst plateaus in southern Mexico and northern Guatemala, whereas the GSHN is associated with landscapes formed by volcanic activity in southern Guatemala, El Salvador, Honduras and Nicaragua. At least seven limnological subregions were identified, illustrating the high heterogeneity of aquatic systems in the northern Neotropics. Analysis of ostracode species assemblages shows that water chemistry and mineralogical attributes of the host environments drives species composition (distribution). Low ostracode species richness in the northern Neotropics also seems to be strongly related to the geological history of the region. The low number of species per lake contrasts with the number of species per lake in temperate regions, which is at least five times higher. Questions about the applicability of the Latitudinal Diversity Gradient theory for Ostracoda and other zooplankton and zoobenthos groups remain unresolved, and sampling in the Neotropics and other tropical regions of the world is necessary. SEM analysis highlights that geodiversity has a direct influence on limnological regions, and an indirect but relevant influence on freshwater ostracodes. This is the first study to integrate data on watershed geology, physical and chemical characteristics of the water column, sediment mineralogy and geochemistry, and biota in aquatic ecosystems of southern Mexico and Central America. Further studies should focus on establishment of a more detailed regionalization, by including a greater number of lakes, more environmental variables, and samples collected at different times throughout the seasonal cycle.

Data availability. Water physico-chemical, sediment geochemistry, mineralogical and geological data from the 76 aquatic ecosystems sampled in this study are available in Table S1 in the Supplementary Material and in the Pangaea repository: https://doi.org/10.1594/PANGAEA.940538. Ostracode relative abundances at each sampling site can be found at the Pangaea repository: https://doi.org/10.1594/PANGAEA.940254.

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