

Novel responses of diatoms in neotropical mountain lakes to indigenous and post-European occupation



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ABSTRACT

How Indigenous peoples and European settlers transformed terrestrial ecosystems in the Americas is well evidenced in the literature, but far less is known about how aquatic ecosystems changed. This study examined diatom records from sediment cores from paleoclimate studies in mountain lakes of Guatemala, Panama, and Colombia, in order to clarify the long-term human influences on the ecology of these lakes. We focused on two aspects of beta diversity in identified diatom zones: species turnover and variation in relative abundances of species. All records displayed a single diatom zone or cluster of zones with assemblages that had no close analogues in the past. The ages of these distinctive assemblages varied from post-European to 5000 cal yr BP. Most novel assemblages comprised moderately motile, non-planktonic, single-celled diatoms, associated with disturbed, productive environments. Archaeological data and pollen records pointed to the onset of intensification of human activities as the main driver behind the changes in diatoms. Maximum depth exerted control on how diatom communities responded to anthropogenic stressors. In shallower lakes, diatom assemblages transitioned gradually over time into their current novel composition. In deeper lakes, assemblages displayed slight fluctuations before shifting to their current condition. Differences between the two lake groups likely resulted from a more complete water-column mixing and higher rates of nutrient cycling in the shallow lakes, which led to a more rapid response of the diatoms to environmental changes. The shift to novel recent diatom assemblages suggests that these lakes now display ecosystem characteristics with no past analogues, and that they have lost their capacity to resist change or recover from stressors, jeopardizing the future of mountain water resources.

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1. Introduction

Consensus is growing that modern ecosystems are the product of millennia of human-environment interactions (Dodson, 2010; Power et al., 2018). Before European settlement in the tropical Americas in the 1400s, Indigenous peoples had already altered

landscapes (Anselmetti et al., 2007; Castilla-Beltrán et al., 2018; Erickson, 2008; Flantua et al., 2016; Hooghiemstra et al., 2018; Metcalfe et al., 2007; Sluyter, 2001). Forests were cleared for agriculture and construction, and the well-documented, protracted droughts associated with the 9th-century Late Classic Maya cultural collapse in southern Mexico and Central America likely resulted from widespread vegetation removal that altered the regional precipitation regime (Cook et al., 2012). Others have also suggested that, when areas deforested and/or cultivated by Indigenous peoples were abandoned in the early 16th century, largely as a consequence of introduced European diseases, i.e. the “Great Dying,” widespread forest re-growth and consequent absorption of atmospheric carbon dioxide (CO₂) led to the Little Ice Age (Koch et al., 2019; Loughlin et al., 2018). The biogeography and enormous biodiversity of the Amazon Basin are not solely the result of natural processes, but rather, a consequence of human-environment interactions that occurred over thousands of years. During this time, local Indigenous peoples managed the forests, water, and soils, using sophisticated techniques that included construction of irrigation canals, land terracing, and production of *terra preta* (Amazon dark soil) (Erickson, 2008; McMichael et al., 2012). After the “Great Dying,” European-style agriculture was introduced, and many areas in the Americas were again cleared for pasture, row crops, and mineral extraction, with profound consequences for terrestrial ecosystems (Etter and van Wyngaarden, 2000; Hooghiemstra et al., 2018; Loughlin et al., 2018). Native forests were altered and new ecological dynamics emerged as a consequence of the introduction of exotic plants and large herbivores. For instance, cattle were new to the Americas and were capable of eating young trees, thereby preventing forest re-growth in some areas, leading to the development of open forests and treeless grasslands across many regions of Central and South America (Caetano-Andrade et al., 2019; Castilla-Beltrán et al., 2018; Etter et al., 2008; Hooghiemstra et al., 2018).

Paleolimnological studies in the Americas indicate that lakes and rivers subjected to human influence received greater sediment and nutrient inputs from anthropogenic deforestation and soil erosion, and that the additional sediment reduced water clarity and altered natural biogeochemical cycles, e.g. nitrogen and phosphorus (Brugam and Muñoz, 2018; Castilla-Beltrán et al., 2018; Clement and Hoorn, 2001; Dubois et al., 2018; Frisch et al., 2014; Hooghiemstra et al., 2018; Metcalfe et al., 1991; Sowers and Brush, 2014; Vélez et al., 2011). Very few paleolimnological studies in southern Central and northern South America, however, have focused on understanding the responses of lakes themselves to human activities. Whereas abundant evidence exists for the profound influence of pre-Hispanic cultures and European settlers on terrestrial ecosystems in these tropical areas, little is known about how humans have affected aquatic ecosystems.

Nevertheless, a few studies suggested that aquatic organisms responded differently, depending on the degree of human influence. For instance, a plant macrofossil study in Lake Fúquene, Colombia, today a highly eutrophic water body dominated by water hyacinths (*Eichhornia crassipes*) and Brazilian elodea (*Egeria densa*), showed that increases in nutrient load and reductions in water levels from hydrologic diversion for irrigation resulted in the loss of native aquatic plants, whereas a few invasive, exotic species expanded and eventually came to dominate (homogenization) (Salgado et al., 2019). In contrast, diatom assemblages in a group of less human-influenced, highland lakes in Ecuador showed little compositional change over the last 150 years (Benito et al., 2019; Giles et al., 2018).

Accordingly, we examined the following research questions, using diatom records from a suite of shallow and deep Neotropical mountain lakes previously collected that ranged in degree of past human influences. First, how have long-term (centuries to millennia) anthropogenic impacts affected Neotropical mountain lakes? And second, how have diatom responses to anthropogenic impacts differed among lakes? We have three working hypotheses: (1) human activities altered water supply and lake levels, increased runoff and sediment and nutrient inputs to the lakes (Anderson, 2014), changing the diatom community through increased water turbidity, shading, eutrophication, and habitat alteration; (2) human-mediated changes eventually led to a different and more homogenous diatom assemblages, as seen for aquatic macrophytes (Salgado et al., 2018); (3) the trajectory to a more homogenous diatom community differed between shallow and deep lakes, linked to the different mixing regimes and macrophyte cover.

2. Methods

We analyzed data for diatoms from sediment cores previously collected to study long-term climate and environmental variations in mid- and high-elevation lakes in the Neotropics using several statistical approaches. We chose the diatom datasets using several criteria. We sought records: (1) from shallow ($z_{\max} < 7$ m) and deep ($z_{\max} > 14$ m) lakes at middle to high elevations (all > 780 m above sea level (asl)). Records from lowland lakes can be affected by complex hydrologic dynamics that make identification of specific environmental stressors difficult; (2) that extend back several millennia prior to European arrival; (3) with reliable radiocarbon chronologies (Flantua et al., 2016); and (4) from lakes with a modern gradient of human influence in their watersheds. We performed statistical analyses on diatom relative abundances in samples, for which a minimum of 400 valves had been counted. All species names were updated using the websites Diatom.org, and AlgaeBase.org. Details on taxonomic classification and paleoenvironmental interpretation are found in Supplementary Information

Table 1

Names, locations and morphometric characteristics of the selected study lake types (deep or shallow), along with maximum age for each sediment record, local vegetation cover, tropic status and citation for the original publication in which the diatom records were published.

Lake type	Record	Country	Max age (cal yr BP)	Altitude (m asl)	Surface area (km ²)	Max depth (m)	Vegetation cover	Current trophic status	Original reference
Deep ($z_{\max} > 14$ m)	Amatitlán	Guatemala	2400	1186	15.2	33	Forest	Hypereutrophic	Vélez et al., 2011
	San Carlos	Panama	1080	780	0.04	8	Forest	Eutrophic	Correa-Metrio et al., 2016
	Ubaque	Colombia	4100	2179	0.10	14	Forest	Eutrophic	Bird et al., 2017
	Pedro Palo	Colombia	8000	2000	0.2	20	Forest	Mesotrophic	Vélez et al., 2021
	La Cocha	Colombia	13,700	2780	40.5	75	Forest/ Páramo	Oligotrophic	González-Carranza et al., 2012
Shallow ($z_{\max} < 7$ m)	Fúquene	Colombia	23,770	2540	30	7	Forest/ Páramo	Hypereutrophic	Vélez et al., 2003
	Santurbán-Berlín	Colombia	27,600	3800	0.04	<1	Páramo	Oligotrophic	Patiño et al., 2020
	Siscunsi	Colombia	2860	3687	0.5	4.2	Páramo	Mesotrophic	Temoltzin-Loranca, 2018

(SI) Table 1. In this study, we further classified the diatoms according to their motility (Section 2.3).

Mountainous water bodies in the Neotropics range from ephemeral pools and bogs to shallow and deep lakes. Thus, assessments of the effects of humans on aquatic ecosystems in the region are challenging. In an attempt to identify how lake depth influences diatom responses to human influence, we divided the lake dataset into shallow ($z_{\max} < 7$ m) and deep ($z_{\max} > 14$ m) water bodies (Table 1). Selected deep lakes included Amatitlán in Guatemala, San Carlos in Panama, and Ubaque, Pedro Palo, and La Cocha in the Eastern Cordillera of Colombia (Fig. 1). Shallow lakes included Santurbán-Berlín, Fúquene, and Siscunsi, all in the Eastern Cordillera of Colombia (Table 1, Fig. 1).

The analysis utilizes diatom records and sediment lithologic descriptions in previous publications, which also contain descriptions of characteristics of the study sites (Table 1). Sediment records from Lakes Pedro Palo and La Cocha contain only pre-European deposits because uppermost sediments from these lakes were not recovered.

2.1. Core chronologies

We used published chronologies and age-depth models based on Bayesian statistics that employed Bacon software (Blaauw and Christen, 2011) for Lakes San Carlos, Ubaque, Siscunsi, Santurbán-Berlín and Pedro Palo (Table 2 SI; Table 1). Previous age models for cores from Lakes Amatitlán, Fúquene and La Cocha were developed with linear interpolation. We produced new chronologies using Bacon and the ^{14}C dates from the original publications (SI Table 2). All radiocarbon dates are reported in calibrated years BP (cal yr BP), rounded to the nearest decade.

2.2. Statistical analyses

Sediment samples that lacked diatoms were removed prior to statistical analyses and diatom counts were square-root-transformed to weight the relative importance of rare vs. abundant species (Legendre and Gallagher, 2001). Major zones of diatom change, reflecting characteristic diatom assemblages, were identified in each core by Constrained Hierarchical Clustering analysis on chord distances, performed using the *chclust* function (*coniss* method) of the *rioja* package (Juggins, 2009) in R (R Development Team, 2016). Supplementary Information SI Figure 1 presents clusters per each record.

Temporal shifts in abundance and species composition (Beta diversity; Whittaker, 1960) display greater variation in biological communities in response to human-driven environmental change than measurements of species richness alone (Anderson et al., 2011; Legendre and De Cáceres, 2013). Although workers have proposed different measures of beta diversity to express that variation (Anderson et al., 2011; Legendre and De Cáceres, 2013; Tuomisto, 2010a,b), recent analyses suggest that, when possible, beta diversity studies should focus on two complementary aspects of community structure (Anderson et al., 2011), *turnover* - the directional change in assemblage composition from one sampling unit to another along a temporal gradient, and *assemblage heterogeneity* - the variation in assemblage composition arising from shifts in species identities and abundances among groups of sampling units over time. Use of these two measures of beta diversity in concert helps reveal the underlying nature of patterns in β diversity that arise simultaneously from presence/absence data and relative abundance information (Anderson et al., 2011). We therefore focused the statistical analyses on these two

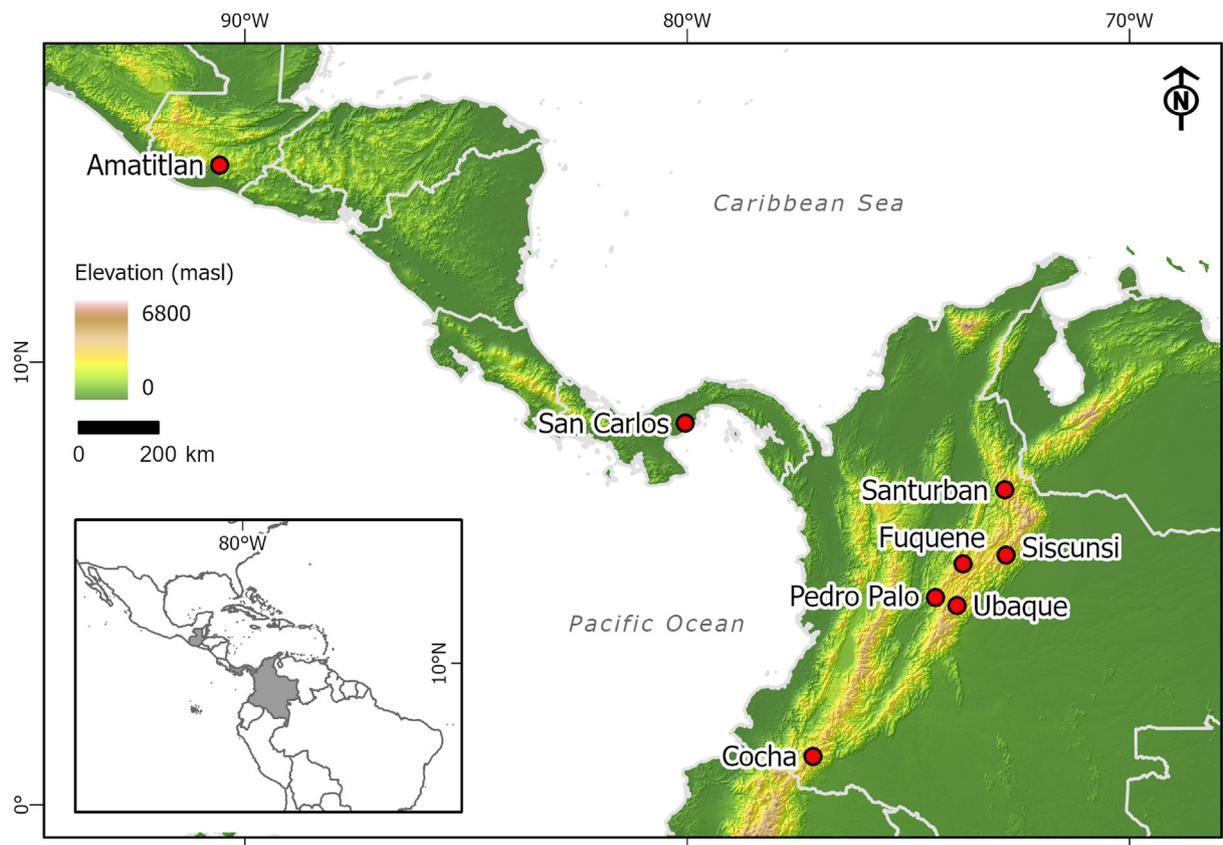


Fig. 1. Geographic locations of the study lakes. Inset map, indicates in grey color the countries in Central and South America in which the study lakes are located: lake Amatitlán in Guatemala, lake San Carlos in Panama (Central America) and lakes Santurbán-Berlín, Fúquene, Pedro Palo, Ubaque, Siscunsi and La Cocha in Colombia (NW South America).

complementary aspects of beta diversity by undertaking the combined approaches of Principal Coordinate Analysis (PCoA), Homogeneity Analysis of Multivariate Dispersions (HMD; Anderson, 2006) and Permutational Analysis of Variance (PERMANOVA; Anderson, 2001). PCoA enabled visual assessment of trajectories in the diatom assemblages (turnover) between samples at each lake. HMD analysis was suitable for assessing the significance of assemblage heterogeneity attributed to variation in relative abundances of species, and PERMANOVA enabled assessment of the significance of the compositional heterogeneity attributed to variation in the identity of species (turnover) present.

HMD analysis is a non-parametric method that compares variability of mean distance to a centroid (dispersion) within temporally predefined groups, to variability in this distance between the predetermined groups in a PCoA. We thus defined the variation in assemblage heterogeneity as the distance to the spatial median of the dissimilarities in diatom species relative abundances among sediment samples, grouped respectively, within the major temporal zones of change (groups) detected by hierarchical cluster analysis. We assumed a zone with higher values of mean distance to the group median as characterized by greater variability (greater multivariate dispersion) in diatom

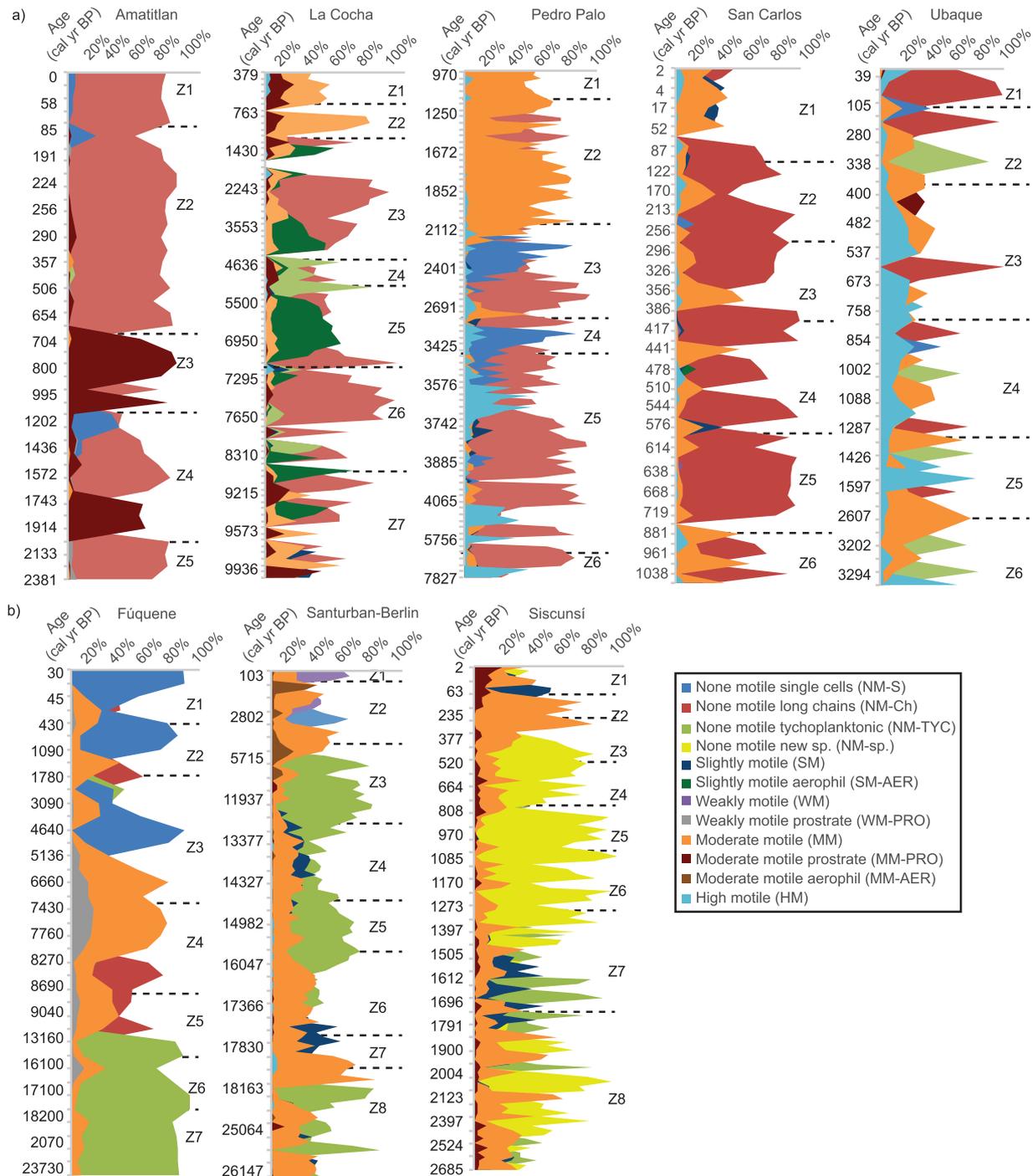


Fig. 2. Relative proportions of motile and non-motile diatoms in each record, along with the zones determined by cluster analysis (black dashed lines) for (a) deep and (b) shallow lakes.

species abundance between the sediment samples, and hence, greater temporal assemblage heterogeneity (Anderson et al., 2006; Salgado et al., 2018). Conversely, low multivariate dispersion (lower mean distance to the group median) indicates a more homogenous assemblage structure. We conducted an overall HMD analysis for each lake, treating each zone as an independent group. Differences between zone pairs were then tested *post hoc* using the Tukey honest test (499 permutations, $p < 0.05$) to determine specifically which zones differed in diatom assemblage heterogeneity from one another. HMD analyses were performed using the *betadisper* function in the *vegan* package (Oksanen et al., 2013) and results were plotted using boxplots and PCoA plots.

Although HMD analysis provides a robust measure of compositional heterogeneity, it does not discriminate between samples that differ in species composition only, i.e. two zones of diatom change could be equally heterogeneous/homogenous, but differ significantly in species composition (Anderson et al., 2011). Therefore, we used PERMANOVA (*adonis* function in *vegan* package R; Oksanen et al., 2020) to explore species compositional differences between assemblages. PERMANOVA is a non-parametric method for multivariate analysis of variance that compares the variability of average dissimilarity within groups, versus the variability among groups, using the ratio of the F-statistic through permutational tests.

2.3. Diatom responses to human activity

To understand the response of diatom communities to human activities, we also grouped individual diatom species from each lake into two broad functional groups based on their motility. Table 1 SI presents the classification for dominant species. If a given diatom was not classifiable at the species level, we grouped it according to its genus, following Berthon et al. (2011). *Non-motile* (NM) diatoms lack movement and include mainly planktonic forms. This group was further subdivided into: (i) non-motile diatoms that form long chains (NM-Ch), such as *Aulacoseira* spp., (ii) non-motile, single-cell diatoms that do not form chains (NM-S), like *Cyclotella* and *Discostella* spp., and (iii) diatoms that may or may not form long chains, but are tycho planktonic, that is, live in both the plankton and benthos (NM-TYC). These include pioneer diatoms such as *Pseudostaurosira brevistriata*, *Staurosira construens* and *Staurosirella pinnata* (formerly *Fragilaria brevistriata*, *F. construens* and *F. pinnata*, respectively) (Biskaborn et al., 2012). NM-Ch and NM-TYC are often associated with productive environments (Passy, 2007), whereas NM-S are generally associated with water turbulence and highly productive environments (Passy, 2007).

The second functional group, *Motile diatoms* (M), comprises diatoms with active movement. When more information on species was available, we subdivided them into Slightly Motile (SM), Weakly Motile (WM), Moderately Motile (MM), and Highly Motile (HM), following the ecology presented in Diatoms.org. These include several species of *Nitzschia*, *Gomphonema*, *Encyonema*, *Eunotia* and *Pinnularia*. When possible, we also noted if the species grew prostrate, that is, on the substrate surface with the entire valve attached (*Motile Prostrate* [M-PRO]), as is the case for *Achnanthisidium minutissimum* and *Cocconeis placentula* (Passy, 2007; Berthon et al., 2011), or if the species were aerophilous (*Motile Aerophilous* [M-AER]), such as *Diploneis elliptica*. These species grow in soils and are adapted to periods of desiccation. M-PRO can tolerate water turbulence and other disturbances.

Under increasing anthropogenic activity in the watershed and associated soil erosion, an increase in input of detrital sediments and nutrients to the lakes would be expected. These physical perturbations would favor the increase or even dominance of

motile and non-motile single-celled diatoms. Motile species can avoid physical disturbances such as erosion-generated turbidity, shading, and burial (Jones et al., 2014), while also seeking favorable nutrient-rich habitats like those that result from input of soil nutrients (Passy, 2007). Single-celled diatoms are common in environments characterized by water turbulence, and in habitats with abundant macrophytes (Berthon et al., 2011), like those that result from eutrophication and or a decrease in water level.

3. Results

3.1. Deep lakes

3.1.1. Lake Amatitlán, Guatemala (1186 m asl)

Cluster analysis identified five diatom zones of community change spanning the last ca. 2400 years (Fig. 2a). Zones 5–4 (2380–1330 cal yr BP) and zone 2 (700–190 cal yr BP) comprised non-motile planktonic *Aulacoseira granulata*, *Fragilaria delicatissima*, planktonic single-celled *Discostella stelligera* and moderately motile, prostrate *Nitzschia amphibia* and *N. palea*, and spanned the Pre-Classic and Classic Maya archaeological periods. Zone 3 (1200–750 cal yr BP) corresponded to the Terminal Classic Maya period associated with the Maya “collapse,” and part of the Postclassic. The period is dominated by moderately motile, prostrate *N. palea* and *N. amphibia* var. *rostrata*. Zone 1 (110 cal yr BP-Present) is dominated by *A. granulata*, with significant increases in non-motile single-celled *Cyclotella meneghiniana*, tycho planktonic *Ulnaria ulna*, *F. delicatissima*, and the first appearance of *Fragilaria crotonensis*.

HMD analysis showed that temporal shifts in diatom assemblages were accompanied by a significant ($p = 0.005$; $F = 4.5157$) gradual decline in assemblage heterogeneity over time (Fig. 3a). More heterogeneous assemblages (greater mean distance to the centroid) occurred in zone 5, whereas recent zone 1 was more homogenous (Fig. 3a). The Tukey test revealed that the following zones were significantly different: zones 5 and 1 ($p = 0.02$), and zones 5 and 2 ($p = 0.004$). Diatom assemblages in zone 3 appeared more distant from zones 5, 4 and 2 in the multivariate PCoA space, by clustering on the right-hand side of PCoA axis 1. Similarly, diatoms from zone 1 were clustered away from the older zones, along the negative portion of PCoA axis 2. PERMANOVA showed that with the exception of zones 5 and 4, all remaining zones were significantly different from one another with respect to diatom species composition (Fig. 3a; Fig. 2 SI).

3.1.2. Lake La Cocha, Colombia (2780 m asl)

Cluster analysis identified seven diatom zones extending back to the early Holocene (Fig. 2a). The early and middle Holocene are represented in zones 7 to 4 (10,480–4640 cal yr BP), the late Holocene in zone 3 (4340–1430 cal yr BP), and the last 1430 years in zones 2 and 1. Zones 7–3 (10,480–1430 cal yr BP) are characterized by non-motile species *A. ambigua*, aerophilous *Orthoseira rooseana* and *Humidophila contenta*, and tycho planktonic *P. brevistriata*. Zones 2 and 1 (the last 1430 years) display an increase in the moderately motile aerophilous *Diploneis elliptica* and in moderately motile species of *Cymbella*, *Frustulia*, *Pinnularia* and *Eunotia* (Table 1 SI).

HMD analysis showed that the temporal shifts in diatom assemblages were accompanied by significant ($p < 0.001$; $F = 6.7508$) variation in assemblage heterogeneity over time. More heterogeneous assemblages occurred in zones 7 and 2, whereas more homogenous assemblages characterized zones 5 and 1 (Fig. 3b). The Tukey test revealed that the following zone pairs are significantly different: zones 1 and 7 ($p = 0.005$), zones 4 and 5 ($p = 0.02$), zones 5 and 7 ($p < 0.001$), and zones 6 and 7 ($p < 0.001$). The PCoA plot (Fig. 3b) showed that from 10,480–1430 cal yr BP

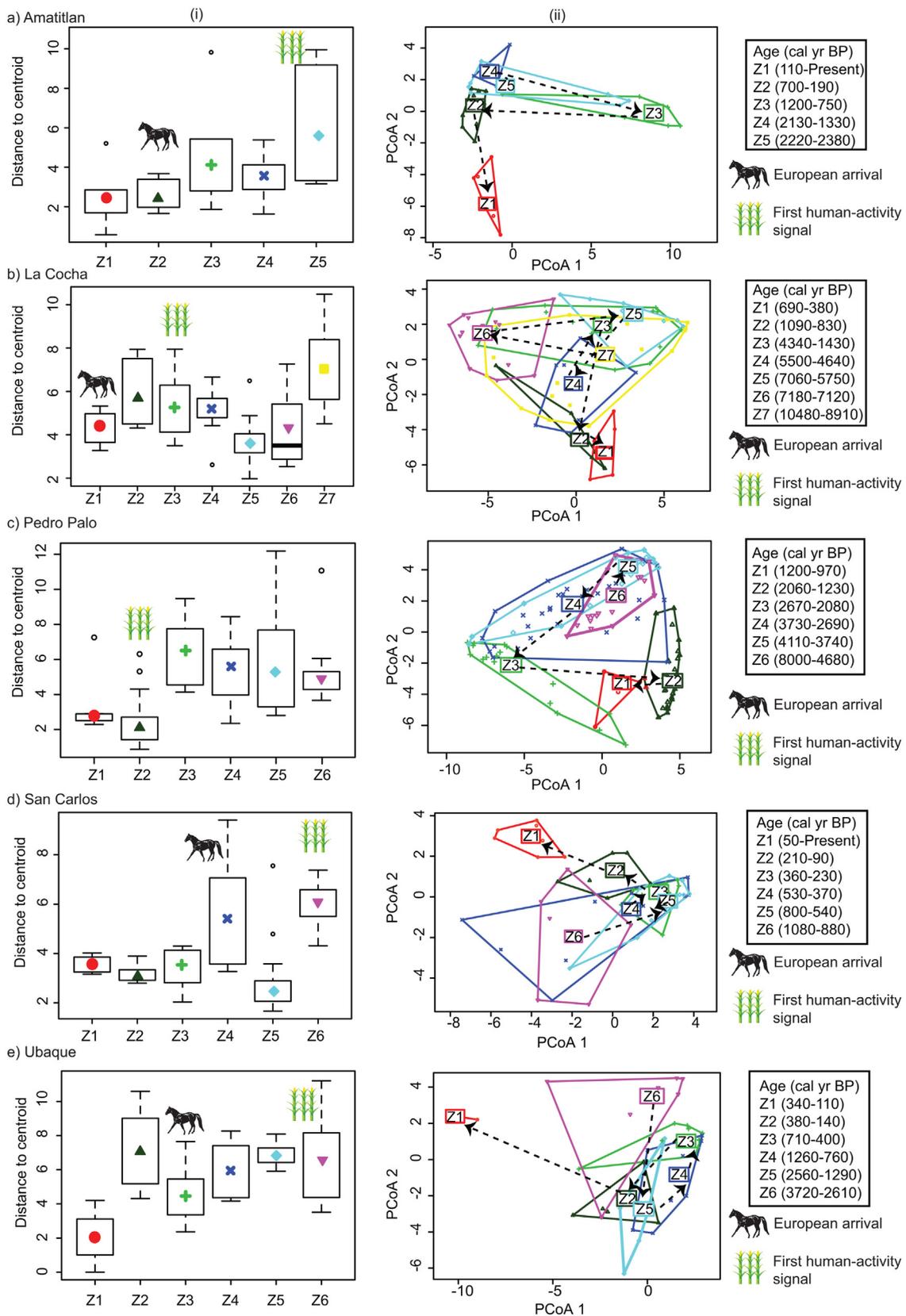


Fig. 3. Results of HMD analyses for the deep lakes: a) Amatitlán, b) La Cocha, c) Pedro Palo, d) San Carlos, and e) Ubaque. (i) boxplots of the variation in diatom assemblages and the distance to mean value in each zone determined by cluster analysis, (ii) variation of the diatom assemblages and their distance to the spatial median in the ordination space (PCoA). Zones, determined by cluster analysis, and presented in age order from oldest to youngest, are identified by specific symbols: zone 1 (red circle), zone 2 (triangle), zone 3 (cross), zone 4 (x), zone 5 (diamond), zone 6 (inverted triangle), and zone 7 (square). Ages of the zones and legend for the onset of human activities and European arrival are presented on the right.

(zones 7 to 3), diatom assemblages were relatively more similar in composition and thus appeared closer in PCoA space. Zones 2-1 clustered together, but were distant from previous zone 3, in a similar fashion to Amatitlán. PERMANOVA indicated that all zones differed significantly from one another in terms of diatom species composition (Fig. 3b; Fig. 2 SI).

3.1.3. Lake Pedro Palo, Colombia (2000 m asl)

Cluster analysis identified six diatom zones in the record spanning the last 8000 cal yr (Fig. 2a). Zone 6 (8000–4680 cal yr BP) is dominated by planktonic *A. granulata* var. *angustissima*, with prostrate, epiphytic *C. placentula*; zones 5 to 3 (4110–2080 cal yr BP) are composed of planktonic, single-celled *Discostella stelligera*, *D. pseudostelligera* and chain-forming *F. crotonensis*, and zones 2 and 1 (2060–970 cal yr BP) are composed of moderately motile and epiphytic *Encyonema minutum* and planktonic *A. granulata* var. *angustissima* (Table 1 SI).

HMD analysis showed that temporal shifts in the diatom assemblages were accompanied by a significant ($p < 0.001$; $F = 13.979$) reduction in community heterogeneity in zones 2 and 1 (Fig. 3c). Accordingly, the Tukey test revealed these two more

recent zones differ significantly ($p < 0.05$ in all cases) from zones 6–3. The PCoA plot indicates that the diatom community started to transition into a new compositional association after zone 3 by moving away from the other historical zones (6–4) along PCoA axis 1 and 2. PERMANOVA indicated that all zones differed significantly from one another in terms of diatom species composition (Fig. 3c; Fig. 2 SI).

3.1.4. Lake San Carlos, Panama (780 m asl)

Cluster analysis identified six main diatom zones spanning the last ~1000 cal yr (Fig. 2a). Zones 6 to 3 (1080–230 cal yr BP) have similar diatom assemblages (Fig. 3d), dominated by planktonic *F. crotonensis*, with peaks in *A. granulata*, and moderately motile species such as *Navicula lanceolata*, *Gomphonema* spp. and *Eunotia* spp. Zone 2 (210–90 cal yr BP) contains the first peak in planktonic, single-celled *D. stelligera*. In zone 1 (50 cal yr BP-Present) the composition is significantly different and includes slightly motile *Achnanidium exiguum* var. *constricta*, *A. minutissimum* (formerly *Achnanthes exigua* and *A. minutissima*, respectively), and benthic, moderately motile *Encyonema silesiacum* (formerly *Cymbella silesiaca*) and *N. amphibia* (Table 1 SI).

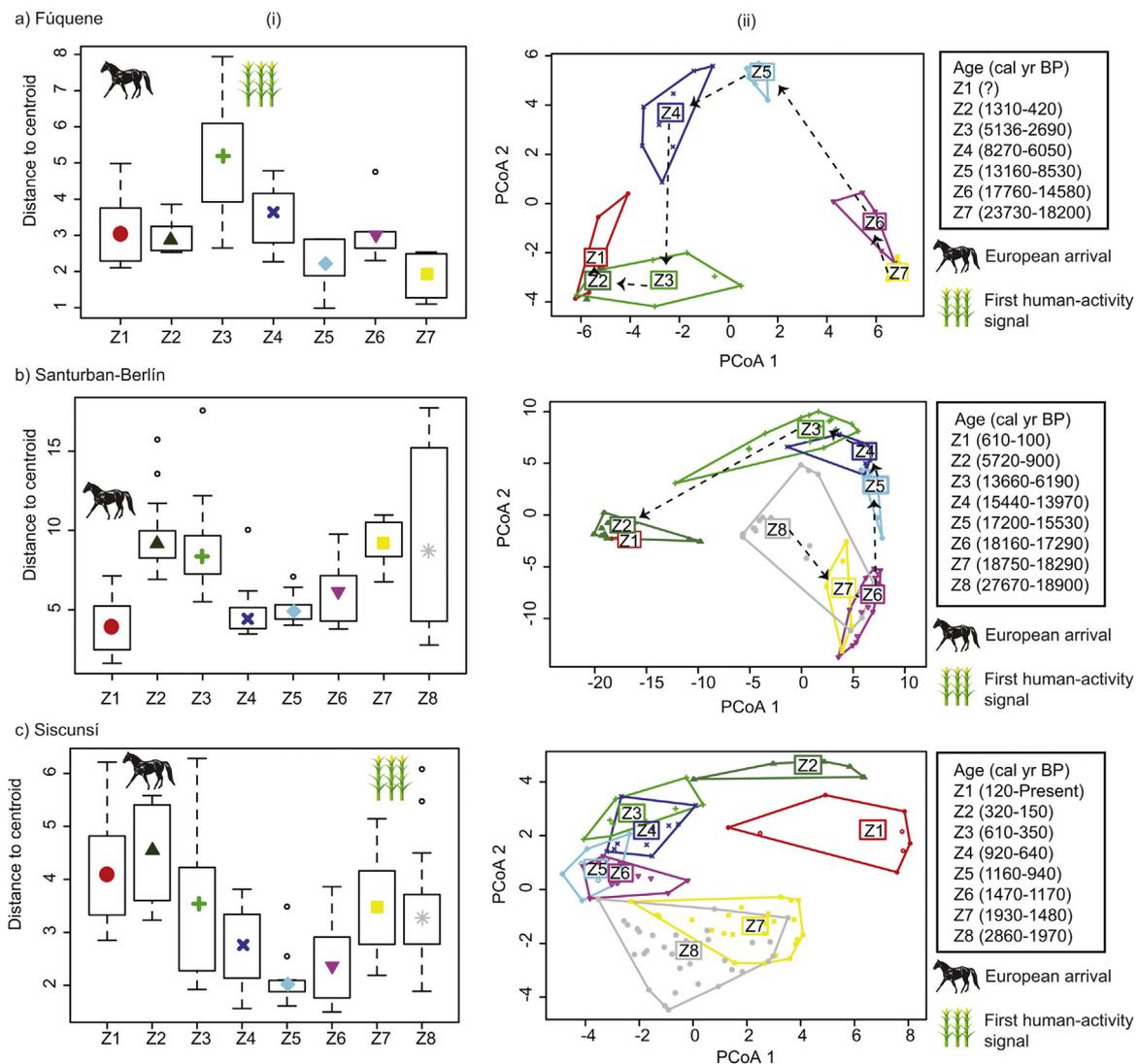


Fig. 4. Results of HMD analyses for the shallow lakes: a) Fúquene, b) Santurbán-Berlín and c) Siscunsi. (i) boxplots of the variation in diatom assemblages and the distance to mean value at each zone determined by cluster analysis. (ii) variation of the diatom assemblages and their distance to spatial median in the ordination space (PCoA). Zones (determined by cluster analysis) are denoted by specific symbols: zone 1 (red circle), zone 2 (triangle), zone 3 (cross), zone 4 (x), zone 5 (diamond), zone 6 (inverted triangle), zone 7 (square) and zone 8 (star). Ages of the zones and legend for the onset of human activities and European arrival are presented on the right.

HMD analysis showed that temporal shifts in the diatom assemblages were accompanied by a significant ($p < 0.001$; $F = 6.2169$) gradual reduction in community heterogeneity over time, with more heterogeneous assemblages occurring in zones 6 and 4 and more homogenous assemblages characterizing the remaining zones (Fig. 3d). The Tukey test revealed that the following zone pairs were significantly different: zones 1 and 6 ($p = 0.03$), zones 2 and 6 ($p = 0.01$), zones 3 and 6 ($p < 0.016$), and zones 5 and 6 ($p < 0.001$). The PCoA plot indicated that the diatom assemblage in zone 1 is more distant from the previous zones along the positive portion of PCoA axis 2. PERMANOVA indicated that diatom species composition among zones 2–4, 3–4, 3–5, 4–5, 4–6 were highly similar and that zone 1 was significantly different from all other zones (Fig. 3d; Fig. 2 SI).

3.1.5. Ubaque Lake, Colombia (2179 masl)

Cluster analysis identified six main diatom zones spanning the last ca. 3700 cal yr (Fig. 2a). Zones 6–3 (3720–400 cal yr BP) are composed of peaks of planktonic *A. ambigua* and variable appearances of non-motile tycho planktonic *Staurisirella pinnata*, *Pseudostaurisirella elliptica*, and planktonic *Fragilaria tenera*, *F. crotonensis* and *C. meneghiniana*. Zone 2 (380–140 cal yr BP) is dominated mainly by *S. pinnata* and zone 1 (110 cal yr BP–Present) includes significant peaks of planktonic *A. ambigua* and a peak in *C. meneghiniana*, with increases in abundance of prostrate valves of colonizer *Achnanthisidium* and *Planothidium* species (Figs. 2a and 3 e, Table 1 SI).

HMD analysis showed that temporal shifts in the diatom community were accompanied by a significant ($p = 0.007$; $F = 3.8537$) gradual reduction in community heterogeneity over time, with more heterogeneous assemblages in zones 6 and 2 and more homogenous assemblages in zones 5, 4, 3 and 1 (Fig. 3e). The Tukey test revealed that the following zone pairs are significantly different: zones 1 and 2 ($p = 0.02$), zones 1 and 5 ($p = 0.02$), and zones 1 and 6 ($p = 0.03$). The PCoA plot indicated that the diatoms in zone 1 are more distant from the previous zones, along PCoA axis 2, and in turn that they are more similar between themselves. PERMANOVA indicated that diatom composition differed significantly among all zones (Fig. 3e; Fig. 2 SI).

3.2. Shallow lakes

3.2.1. Lake Fúquene, Colombia (2540 m asl)

Cluster analysis identified seven main diatom zones spanning the last 23,730 cal yr (Fig. 2b). Zones 7 and 6 (23,730–14,580 cal yr BP) correspond to the last glacial and are composed of non-motile tycho planktonic species like *P. brevistriata* and *S. pinnata*. Zones 5 and 4 (~13,160–6050 cal yr BP) correspond to the early and middle Holocene, and are composed of planktonic *Aulacoseira ambigua*, with benthic and motile species *Encyonopsis microcephala* (formerly *Cymbella microcephala*) and *N. amphibia*. Zones 3 to 1 (last ca. 5000 cal yr) are marked by the dominance of planktonic *D. stelligera* and isolated peaks in the abundance of other planktonic species such as *A. distans* cf. *laevisima* and *C. meneghiniana* (Fig. 3a; Table 1 SI).

HMD analysis showed that temporal shifts in the diatom assemblages were accompanied by significant ($p < 0.001$; $F = 6.0227$) variation in community heterogeneity over time, with more heterogeneous assemblages in zone 3 and 2 and more homogenous assemblages in zones 7–5 (Fig. 4a). The Tukey test revealed that the following zone pairs are significantly different: zones 3 and 5 ($p = 0.02$), zones 1 and 5 ($p < 0.001$), and zones 3 and 7 ($p < 0.001$). The PCoA plot indicates that diatom assemblages transitioned over time into new associations (zones 3, 2 and 1), located more distant from earlier zones along the negative portion of PCoA axis 1. PERMANOVA indicated that the diatom composition in zones 3, 2 and 1 was highly similar (Fig. 4a; Fig. 2 SI).

3.2.2. Lake Santurbán-Berlín, Colombia (3800 m asl)

Cluster analysis identified eight diatom zones in the record spanning the last ca. 28,000 cal yr (Fig. 2b). Zones 8 to 3 (27,670–6190 cal yr BP) are composed of variable abundances of non-motile, tycho planktonic *S. pinnata*, *S. construens* and *Gomphonema* cf. *minutum*. Zones 2 and 1 (5720 cal yr BP–Present) are dominated by aerophilous diatoms and weakly motile species rarely present in previous zones, *Eunotia monodon* (dominant) and *A. alpigena*. The upper 10 cm (covering the last 900 years) contains few valves of planktonic and phosphorus-loving *Stephanodiscus oregonicus* and *S. reimeri* (Fig. 4b; Table 1 SI).

HMD analysis showed that temporal shifts in the diatom assemblages were accompanied by a significant ($p < 0.001$; $F = 6.8936$) variation in community heterogeneity over time, with more heterogeneous assemblages in zones 8, 6, 3, and 2, and more homogenous assemblages in zones 5, 4, and 1 (Fig. 4b). The Tukey test revealed that the following zone pairs differ significantly: zones 2 and 4 ($p < 0.001$), zones 2 and 5 ($p = 0.005$), zones 2 and 6 ($p = 0.009$), zones 3 and 4 ($p = 0.003$), zones 3 and 5 ($p = 0.02$), zones 3 and 6 ($p = 0.04$), zones 4 and 7 ($p = 0.03$), zones 4 and 8 ($p = 0.002$), zones 5 and 8 ($p = 0.02$) and zones 6 and 8 ($p = 0.03$). The PCoA plot indicated that diatom assemblages transitioned over time into new associations in zones 2 and 1, more distant from the other historical zones along the negative portion of PCoA axis 1. PERMANOVA indicated that diatom composition differed significantly among all zones (Fig. 4b; Fig. 2 SI).

3.2.3. Lake Siscunsi, Colombia (3687 m asl)

Cluster analysis identified eight main diatom zones spanning the last ca. 3000 cal yr (Fig. 2b). Zones 8 to 3 (2860–350 cal yr BP) are dominated by non-motile *Staurisirella* sp. nov and variable abundances of non-motile, tycho planktonic *S. construens*, and *Punctastriata mimetica*, and prostrate, epiphytic *Cocconeis placentula*. Moderately motile species such as *Stauroneis anceps* and *Sellaphora pupula* are more abundant in zones 6 to 1. In zones 2 and 1, planktonic *Fragilaria tenera*, and moderately motile and prostrate *Gomphonema truncatum*, *G. acuminatum* and tube-forming *Encyonema silesiacum* appear for the first time; other species that increase significantly at the expense of *Staurisirella* sp. nov include prostrate *C. placentula*, and moderately motile, benthic *Planothidium frequentissimum*, *S. pupula* and *G. affine* (Figs. 2b and 4 c; Table 1 SI).

HMD analysis showed that temporal shifts in the diatom community were accompanied by a significant ($p < 0.001$; $F = 7.873$) variation in community heterogeneity over time, with more heterogeneous assemblages in zones 1 and 2 and more homogenous assemblages in zone 5. The Tukey test revealed that the following zone pairs are significantly different: zones 1 and 4 ($p = 0.02$), zones 1 and 5 ($p < 0.001$), zones 1 and 6 ($p < 0.001$), zones 2 and 4 ($p = 0.003$), zones 2 and 5 ($p < 0.001$), zones 2 and 6 ($p < 0.001$), zones 2 and 8 ($p < 0.001$), zones 3 and 5 ($p = 0.01$), zones 5 and 7 ($p = 0.006$), zones 5 and 8 ($p < 0.001$) and zones 6 and 7 ($p = 0.04$). The PCoA plot indicated that diatom communities gradually shifted over time into new associations in zones 2 and 1, which are more distant from the other historical zones along the positive portion of PCoA axis 1. PERMANOVA indicated that diatom species composition differed significantly among all the zones (Fig. 4c; Fig. 2 SI).

4. Discussion

The combined analyses in this study showed that, in each lake, diatom species shifted significantly into recent, more homogenous and distinct assemblages with no past analogues in the sediment record. The trajectory of the assemblages in PCoA space showed that in both shallow and deep lakes, more recent assemblages are

separated significantly from previous assemblages (Figs. 3 and 4). PERMANOVA and HDM also indicated that these new assemblages are compositionally different and more homogenous, except in Lake Siscunsi.

In all lakes, the most recent diatom assemblage zones included taxa that tolerate physical disturbance (e.g. turbidity and/or water level fluctuations), such as single-celled, motile prostrate and moderate motile, and some non-motile forms that prefer nutrient-rich waters, like chain-forming diatoms (Figs. 3 and 4). The timing of the switch to these recent diatom assemblages varied among lakes, but with the exception of Lake Santurbán-Berlín, coincided with evidence for human activities, e.g. fire, deforestation, agriculture, and soil erosion in their respective watersheds, as inferred from charcoal, pollen, and/or sediment lithology (Table 2). The Santurbán-Berlín record showed no evidence for agriculture. The high altitude and dry climate around the lake could have prevented Indigenous peoples from settling there. Therefore, the diatom assemblages in zones 2-1 probably reflected a change from lacustrine to mire conditions, as inferred from multiple variables that were most likely driven by climate change (Patiño et al., 2020).

4.1. Novel diatom assemblages and lake depth

We divided the study lakes into two groups, those with $z_{\max} < 7$ m (shallow) and those with $z_{\max} > 14$ m (deep). Diatom assemblages in the shallow lakes (Fúquene, Siscunsi and Santurbán) transitioned gradually over time into new compositional associations (Fig. 5; Table 2), whereas older assemblages in each of the deeper lakes (Amatitlán, La Cocha, Pedro Palo, San Carlos and Ubaque) showed little change until shifting towards the more recent novel assemblage (Fig. 5).

4.1.1. Deep lakes

In Lake Amatitlán, diatom assemblages prior to European arrival comprised species indicative of high nutrient concentrations, most likely a consequence of soil erosion and physical disturbance from Pre-Columbian human activities in the watershed (e.g. non-motile planktonic *A. granulata* and *F. delicatissima*, motile *N. amphibia* and *N. palea*, and non-motile, single-celled *D. stelligera*). During the Maya Terminal Classic and part of the Postclassic (1200-750 cal yr BP), Lake Amatitlán was pushed into a slightly modified limnological condition (*Nitzschia* spp. dominated

zone 3) indicative of intense physical disturbance, but the diatom assemblage evidently did not cross a threshold, and later recovered by returning to conditions that prevailed throughout the Preclassic and Classic, ca. 2000 BCE-900 CE (Figs. 3 and 4; 5). After European arrival, *F. crotonesis*, a species associated with cyanobacteria blooms in other Guatemalan lakes (Perez et al., 2013) and with anthropogenic eutrophication in Lake Juanacatlán, Mexico (Davies et al., 2018), appeared for the first time in the sediment record, along with an increase in *C. meneghiniana*, a diatom that is tolerant of turbid conditions (Hassan, 2013). Taken together, the results indicate that Lake Amatitlán experienced a long history of anthropogenic influence, in the form of human-mediated nutrient loading, organic pollution and harsh physical conditions such as turbidity, alterations to littoral areas and water level fluctuations. Nevertheless, in the last century, the lake has become hyper-eutrophic as a consequence of intensified human activities, driven in part by rapid population growth and urban expansion of the Guatemalan capital, which lies ~25 km from the lake, and contributes nutrients and sediment to the lake via the inflowing Villalobos River (Vélez et al., 2011).

In Lakes La Cocha, San Carlos and Ubaque, post-European times were characterized by an increase in prostrate and moderately motile species (*Achnantheidium*, *Cymbella/Encyonema*, *Diploneis* species). This functional diatom association suggests that in more recent times, physical perturbations (e.g. changes in water level, increased erosion and delivery of detrital sediments) increased in importance. In Lake La Cocha for instance, the last ~1430 cal yr have been characterized by severe anthropogenic activities, e.g. deforestation by fire (González-Carranza et al., 2012), initially by the Protopasto Indigenous peoples and later by the Pastos (Rappaport, 2011). Increases in water runoff and fine sediment inputs caused by land clearance have been shown to increase both turbidity and nutrient availability (Jones et al., 2014).

In Lake Pedro Palo, highly motile and non-motile single-cell diatoms increased significantly during the most intense period of anthropogenic activity (zones 5-3; Table 2), after which, moderately motile species increased at the expense of non-motile single cell forms (zones 2-1). This change likely reflects a decrease in turbidity and nutrient-rich waters that enabled macrophyte expansion (zones 2-1), after the most intense period of human occupation diminished (Vélez et al., 2021).

Table 2

Timing of the shift to a novel diatom assemblage, total time span of the record, and the date of the onset of human occupation in the watershed, as indicated by other sediment variables, e.g. changes in lithology. Right column indicates if the change to the novel assemblage was gradual over time (shallow lakes), i.e. if the assemblages varied over time among relatively similar associations before shifting to the current novel assemblage, or distinct (deep lakes), i.e. diatoms changed little before switching to the new assemblage (Fig. 5) (Time in thousands of years before present [ka]).

Lake's depth	Lake	Date of shift to novel diatom assemblage (zone[s])	Time span of the record	Proxy for human activity and date of onset	Depth and date of lithological change	Change to novel assemblage
Deep	Amatitlán	0.1 ka; zone 1	2.4 ka	Pollen/Archaeology (land use) Throughout the record	NA	Distinct
	La Cocha	1.1 ka; zones 2-1	14 ka	Charcoal (fire) 1.4 ka	260 cm (~1.4 ka); light to dark brown peat	Distinct
	Pedro Palo	2 ka; zones 2-1	8 ka	Charcoal (fire) 4.0 ka	N/A	Distinct
	San Carlos	0.05 ka; zone 1	1 ka	Pollen (agriculture) Throughout the record	30 cm (0.035 ka) Peat to light clay	Distinct
	Ubaque	0.1 ka; zone 1	3.7 ka	Throughout the record	51 cm (~0.4 ka) Sand to silt	Distinct
Shallow	Fúquene	5 ka; zones 3-1	23 ka	Pollen (deforestation)~6.3 ka	30 cm organic-detrital to peat 275 cm (~5.2 ka) Peat to light clay	Gradual
	Siscunsi	0.32 ka; zones 2-1	2.8 ka	Chl-a (eutrophication) 1.5 ka	51 cm (0.35 ka) silt increases	Gradual
	Santurbán-Berlín	5.7 ka; zones 2-1	27.6 ka	No evidence (pollen)	35 cm (~4 ka) silt to organic mud	Gradual

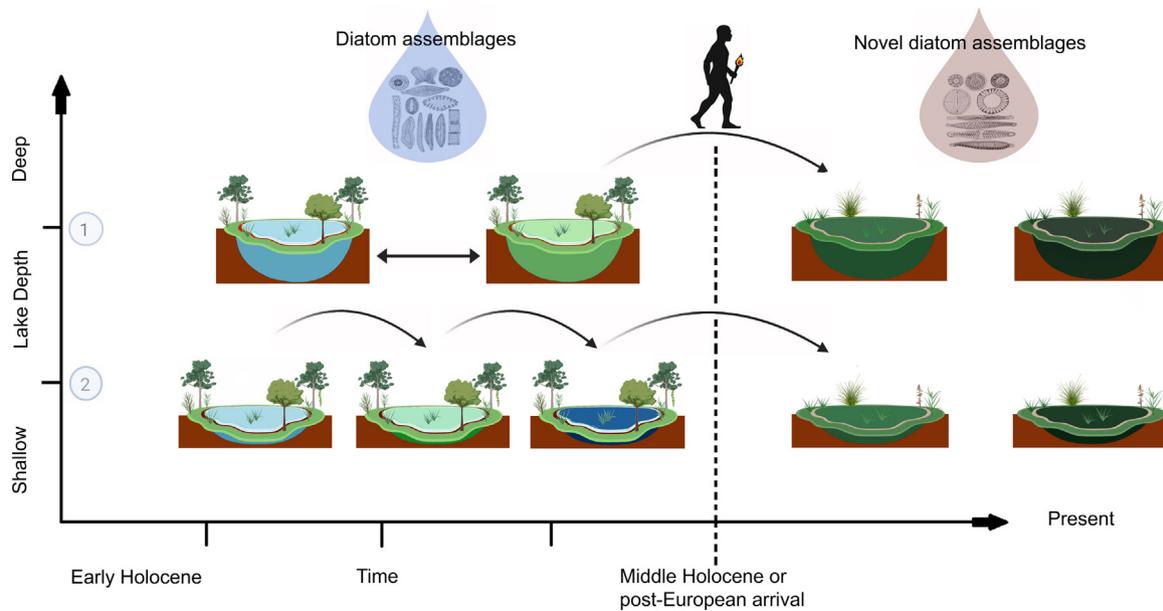


Fig. 5. Conceptual representation of the shift from historical heterogeneous diatom assemblages (grey circles) to recent, more homogenous novel assemblages (black circles): (1) in deeper lakes (Amatitlán, San Carlos, La Cocha and Ubaque), historical diatom communities were grouped under similar compositional assemblages, but then shifted to a new, unique diatom assemblage; (2) in shallow lakes (Fúquene, Santurbán-Berlín and Siscunsi) diatom communities transitioned over time until they reached the current, different assemblage.

Fluctuations in water level alter the extent of the pelagic and littoral areas, thereby changing the abundance and distribution of macrophytes (Talling, 1966), and thus conditions for motile and non-motile diatom taxa. For example, the disappearance of non-motile planktonic diatoms and the increase in motile aerophilous diatoms in the novel assemblage of Lake La Cocha (Fig. 3b) likely reflects fluctuations in the lake's water level and consequent expansion of littoral vegetation. The increase in non-motile, planktonic, chain-forming and single-celled taxa, e.g. *A. ambigua* and *C. meneghiniana*, respectively, and in prostrate species (e.g. *A. minutissimum*) in Lake Ubaque (Fig. 3e), indicates that European arrival affected the lake's water quality, mainly by increasing nutrient concentrations and turbidity.

Although our approach sought to assess the influence of lake depth on diatom community response to stressors, other morphometric factors, as well as hydrology (e.g. water residence time), and the presence/extent of floating or submerged vegetation, as currently observed in the shallow areas of Lake Ubaque, probably also influenced the response of the diatom communities in both shallow and deep lakes (Dubois 2018; Talling, 1966).

Diatom compositional shifts in deeper tropical lakes are probably related to changes in water level, expansion and or contraction of the littoral zone and thermal stratification of the water column (Michelutti et al., 2015; Talling, 1966). Thermal stratification restricts movement of algae between the epilimnion and deeper water layers, contributes to oxygen depletion in the hypolimnion, and if permanent (more likely at high-elevation lakes), prevents nutrient cycling from deep waters, which only occurs with a breakdown of density stratification, normally under cooling conditions (Michelutti et al., 2015; Talling, 1966).

4.1.2. Shallow lakes

In shallow Lakes Fúquene and Siscunsi, earlier times were characterized by non-motile tycho planktonic species (*Staurosira*, *Pseudostaurosira*, *Staurosirella*, *Aulacoseira*), a functional profile commonly associated with mesotrophic (i.e. intermediate nutrient concentrations) environments and littoral conditions (Passy, 2007; Berthon et al., 2011). A combination of non-motile, single-celled

taxa such as *Discostella* and *Cyclotella* species, non-motile planktonic *F. tenera*, moderately motile benthic *Gomphonema* spp., and prostrate *C. placentula*, *Achnantheidium*, and *Planorhynchium* subsequently appeared or increased in the more recent diatom assemblages, after evidence of human activity. These diatom species are often associated with factors such as shading, turbidity, erosion and nutrient increase, suggesting that conditions in these lakes had become more eutrophic and there was greater physical perturbation.

Shallow lakes are often more productive than deeper lakes and are characterized by long-term macrophyte successional dynamics, both spatially and temporally, more complete and frequent water-column mixing (especially in the tropics where this can occur year-round), high rates of nutrient cycling, and smaller water volumes to dilute incoming nutrients (Scheffer, 2001). Therefore, shallower systems often respond more quickly than deeper lakes to climate and environmental changes, catchment degradation and cultural eutrophication (Scheffer, 2001).

Results from this study concur with previous studies that showed that shallow lakes respond earlier and more sensitively to human-related limnological changes than do larger, deeper lakes (Scheffer, 2001). They are, however, at odds with recent findings suggesting that deep lakes in the tropical Andean páramos are more responsive to environmental changes than are small, shallow water bodies (Giles et al., 2018).

4.2. Timing of the change to the novel diatom assemblage

The shift to a novel diatom assemblage in Colombian Lakes Fúquene, Santurbán-Berlín, Pedro Palo and La Cocha, occurred in the middle to late Holocene. Except the relatively undisturbed Lake Santurbán-Berlín, human-mediated deforestation within these lake catchments began in the middle to late Holocene (Table 2). The Indigenous population in what is today Colombia numbered at least five million when Europeans arrived, and some three million of them lived in the Andean region where the lakes are located (Etter and van Wyngaarden, 2000). The region known as the Altiplano Cundiboyacense, where Lakes Siscunsi, Ubaque, Pedro

Palo and Fúquene are located, was densely populated and intensively cultivated since ~5000 cal yr BP (Etter et al., 2008; Delgado, 2016; Reichel-Dolmatoff, 1965; Rodríguez -Gallo, 2019), with constructed raised terraces (*camellones*) surrounded by water-filled channels, which provided food year-round (Rodríguez -Gallo, 2019; Van der Hammen, 2003). The estimated Indigenous population density around Lake Fúquene was 16-33 inhabitants per km², but the human density subsequently rose to 39-78 inhabitants per km² after European arrival (Etter, 2015). Human activities would likely have altered lake water levels, and increased nutrient and sediment loads, contributing to increased turbidity and eutrophication (Anderson, 2014; Jones et al. 2012), which in turn would have made diatom assemblages more homogenous (Salgado et al., 2018).

In records from lakes where Indigenous activities are documented throughout the entire sediment record, i.e. Siscunsi, Ubaque, Amatitlán (Guatemala) and San Carlos (Panama) (Table 2), the shift to the novel diatom assemblage occurred after European arrival (Figs. 3 and 4). This shift suggests that prior to European settlement, diatom communities may have had the ability to resist environmental stress stemming from human activities, while also responding to natural climate disturbances, e.g. changes in precipitation and/or temperature (Correa-Metrio et al., 2016; Vélez et al., 2011, 2003).

In any case, the timing of the change to the novel diatom assemblage occurred long before 1950 CE, a date proposed by some to mark the beginning of the Anthropocene (Zalasiewicz et al., 2017).

4.3. Caveats

Generalizing responses of diatom community to human influence in Neotropical mountain lakes has some limitations. Differences in the time range and temporal sampling resolution among cores from lakes, together with uncertainties in the core chronologies, confound efforts to link shifts in the sediment records with archaeological and historical changes in the watersheds (the latter also subject to dating uncertainties). Further differential diatom preservation and taxonomic approaches among the published and unpublished diatom records could also introduce disparities among paleoenvironmental inferences from lacustrine records. Nevertheless, the multiple independent lines of evidence for drivers of change in diatom communities show general agreement, especially with respect to the development of a novel, recent diatom zone (or zones), that lacks an older analogue. The magnitude and timing of changes observed in our records coincide with what is known about past human occupation of the watersheds, as well as with what is known about past climate changes in the region. Combining the diatom species from each lake into functional groups enabled reduction of the potential influence of taxonomic discrepancies between records. Thus, despite the potential limitations of the paleoecological approach, the data provided important insights into past human-mediated changes in the studied Neotropical lakes.

4.4. Implications for lake management in the "Anthropocene"

The shift to a novel diatom assemblage in the lakes suggests that they have lost or are losing the capacity to resist change or recover from stressors, including human interference and climate change. Implementation of new technologies and intensification of deforestation, agriculture, and urbanization in the catchments were likely the main causes of change in the diatom community (Table 2). Similar to the other lakes, Lake Siscunsi developed a novel diatom assemblage after European arrival. Unlike the other lakes, however, the recent diatom assemblages in Siscunsi became

more heterogeneous. This heterogeneity could reflect a change in land use that occurred after European arrival. According to Temoltzin-Loranca (2018), by 1500 cal yr BP, at the time of the Muisca culture, the lake had become eutrophic (Table 2). The more heterogeneous assemblages that characterized the period following European arrival may indicate subsequent abandonment of the lake catchment and that the lake did not lose its resilience.

The shift in recent times to an unprecedented, more homogeneous diatom assemblage indicates that the lakes have surpassed, or will soon surpass, an environmental threshold (Olden et al., 2004). For the last several decades, Lake Amatitlán has been hyper-eutrophic and plagued with massive cyanobacteria blooms (Perez et al., 2013). Similarly, Lake Fúquene was shown in a precarious state after losing many native submerged macrophyte species (Salgado et al., 2019). The current dominance of invasive plant species, in conjunction with increased eutrophication, renders it increasingly unlikely, from both ecological and economic perspectives, that restoring the lake to its pre-disturbance condition will be possible (Salgado et al., 2019). Homogenization is now considered one of the most prominent forms of biotic impoverishment in freshwater ecosystems worldwide (Rahel, 2002; Olden et al., 2004), and as indicated by the diatom assemblages in the Neotropical mountain lakes studied, might play a significant role in influencing lake food-web structure (Beisner et al., 2003), rates of non-native species spread and community resistance to future invasions (Olden et al., 2004), and loss of resilience in the face of further eutrophication (Salgado et al., 2018) and or climate change (Michelutti et al., 2015).

5. Conclusions

Examination of long-term changes in diatom assemblages in Neotropical mountain lake records produced answers to the research questions posed in this paper. First, we found that human activities, both before and after European arrival, affected the study lakes by pushing them into a novel condition. This different condition was manifested as a shift to unprecedented diatom assemblages that displayed different species composition and were more homogenous (Beta diversity) than assemblages that had inhabited the lakes in earlier times. Lake Santurbán-Berlín was least affected by human activities, and thus the recent shift to a more homogenous diatom community reflects changes in the climate and local environment.

Second, the lakes responded differently depending on their maximum water depth. In shallow lakes ($Z_{\max} < 7$ m), the diatom community changed gradually towards a novel assemblage, whereas in deeper lakes ($Z_{\max} > 14$ m), diatom assemblages fluctuated, but maintained similar species composition, then subsequently shifted to a different assemblage. The differential response of diatom communities may be explained by greater submerged vegetation cover and a more complete water-column mixing and higher rates of nutrient cycling in shallow lakes. Biota in these shallow systems responds more quickly to catchment degradation, sediment input and cultural eutrophication. Other factors that may influence the differential response of diatoms to climate change include differences in lake volume, water residence time and climate change (Giles et al., 2018; Michelutti et al., 2003).

For lakes with diatom records that spanned the Holocene or more (lakes La Cocha, Fúquene and Pedro Palo), the shift to the novel diatom assemblage occurred in the middle to late Holocene, associated with the onset or intensification of human activities. Lakes that yielded shorter records, and were subject to human impacts throughout the time span of the recovered sequence (Amatitlán, San Carlos, Ubaque), showed a pronounced change after European settlement, reflecting the intensification of post-colonial human activities.

Although paleoenvironmental inferences are limited by the time span, sampling resolution, age model, and preservation of fossils in the sediment records, they nonetheless provide invaluable insights into past environments and exploration of ecosystem processes that occur on time scales longer than human life spans. Diatom assemblages indicated that human activities had a profound influence on the ecology of Neotropical aquatic ecosystems and that these lakes have lost or are losing the capacity to resist change or recover from stressors, including human interference and climate change.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ancene.2021.100294>.

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