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A millennium of climatic and floristic dynamics in the Eastern Cordillera of the Colombian Andes

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Abstract

Aim: The transition from the Medieval Climate Anomaly (MCA, 950–1250 CE) to the Little Ice Age (LIA, 1350–1800 CE) is the largest pre-industrial climate shift within the last two millennia, offering an opportunity to study how vegetation responds to rapid climate change. We analysed a sedimentary record from the Colombian Andes to reconstruct regional vegetation dynamics during this time interval, identify the modern environmental distribution of taxa present in the fossil record and provide a reference for modern regional temperature change.

Location: Lake Tota, Eastern Cordillera, Colombian Andes.

Taxon: Angiosperm and Gymnosperms.

Methods: A sediment core was analysed for organic geochemistry and pollen to reconstruct environmental and vegetation variability between 800 and 1800 CE. Modern occurrences of individuals of the genera found in the fossil record were used to model the distribution of taxa across gradients of mean annual temperature and precipitation. These models were used to reconstruct temperature and precipitation across time and evaluate the probability of occurrence of taxa from the fossil record across the contemporary landscape.

Results: Reconstructed regional vegetation dynamics were highly coupled with global temperature patterns. Reconstructed climate showed that conditions were warm and dry during the MCA, and cold and relatively wet during the LIA, although quantitative estimations might have been amplified by human disturbances. Rates of temperature change during the MCA-LIA transition were substantially lower than those calculated for the last two decades. Vegetation turnover between 800 and 1800 CE resembled those expressed through a transect extending ~30 km southeast from the lake.

Main conclusions: Around lake Tota, modern rates of temperature change have no precedent within the last two millennia. The modern environmental affinities of taxa involved in vegetation turnover during the MCA-LIA transition point to the importance of landscape diversity and connectivity for rapid vegetation response to climate change.

KEYWORDS

Andean forest, climate change, Colombian Andes, Eastern Cordillera, little ice age, medieval climate anomaly, paramo, vegetation turnover

1 | INTRODUCTION

The tropical Andes are one of the most biodiverse regions on Earth (Myers et al., 2000). The uplifting of this mountain range created a rugged topography and steep altitudinal gradients that have, in turn, resulted in a high physiographic and biologic diversity (Hooghiemstra et al., 2006; Myers et al., 2000). In northern Colombian, the Eastern Cordillera is characterized by a biodiverse vegetation mosaic that ranges from tropical wet forests in the piedmont to paramo grasslands at altitudes above 3500 m asl, passing through montane tropical forests of various types of composition and structure (Rangel-Ch et al., 1997). Today, anthropogenic activities at global and regional scales pose unprecedented threats to the diversity of this vegetation mosaic (Armenteras et al., 2003; Buytaert et al., 2011) and, thus, on the goods and services these ecosystems provide. Whereas the geographical distributions of many species have been shifting as a result of global change (Freeman et al., 2021), the transformation of the natural vegetation into pastures and cultivated areas poses obstacles to the eventual migration of natural populations (Armenteras et al., 2003; Buytaert et al., 2011).

Through the Quaternary, global and regional climatic variability has resulted in substantial variability of the Andean ecosystems (e.g., Flantua et al., 2019; Groot et al., 2011; Ledru et al., 2013; van der Hammen, 1974). Warmings have caused upslope migration of species and have been usually associated with an invigorated hydrological cycle (Groot et al., 2011). Coolings, on the other hand, have caused downslope migrations and have been usually associated with drier conditions, especially at higher elevations (Flantua et al., 2019; Groot et al., 2011). These responses of vegetation to environmental changes are mostly defined by the length of the life cycle of individuals and the environmental variability of the region, as steeper environmental gradients facilitate migration (Bush, 2002). In the last two millennia, both climatic change and anthropogenic activities have influenced Andean vegetation (e.g., Bird et al., 2011; Correal Urrego & van der Hammen, 1977; Ledru et al., 2013; Polissar et al., 2006; Thompson et al., 2013). However, much of the recent change reflects human occupation patterns that in most cases amplify climatic alterations (Bush et al., 2017). The pollen record of lacustrine sediments offers elements to elucidate compositional and environmental aspects of vegetation dynamics associated with climate and human occupation. The relative importance of these two vegetation drivers in palaeoecological records is strongly influenced by lake size, with small lakes being especially sensitive to human activity (Davis, 2000). Large lakes with large catchment basins, on the other hand, result in a pollen signal that encompasses several vegetation types under diverse successional stages, producing a palynological signal that represents an average of regional vegetation dynamics, which, at decadal-to-millennial time scales, are mostly driven by climatic variability.

We use a sedimentary sequence from Lake Tota, the second largest high-altitude fresh-water body in the Andes located in the Eastern Cordillera of Colombia (Figure 1), to reconstruct regional vegetation changes from ~800 to 1800 Common Era (hereafter CE).

We use modern distribution of genera identified in the fossil record to transform vegetation changes into quantitative estimates of temperature and precipitation. The analysed time interval covers the transition from the Medieval Climate Anomaly (MCA) to the Little Ice Age (LIA), which represents the largest global temperature oscillation during the last two millennia (Ljungqvist et al., 2012). Thus, this period encompasses climatic and ecological variability relevant to understanding modern processes of climate change. The climatic transition represented by the studied time interval, the regional nature of the pollen signal of Lake Tota and the diverse physiography of the region provide an opportunity to study the connections of vegetation changes in space and time. Here we report changes of vegetation and climate in the basin of Lake Tota contextualized in the modern environmental conditions of the region. Accordingly, our questions are as follows: (i) what was the effect of the global temperature variability experienced between the MCA and the LIA on the vegetation around Lake Tota? (ii) How do the taxa that characterized the transition from the MCA to the LIA distribute across the modern temperature and precipitation gradients of the region? and (iii) How do rates of temperature changes between the MCA and the LIA compare with those that characterize modern global warming?

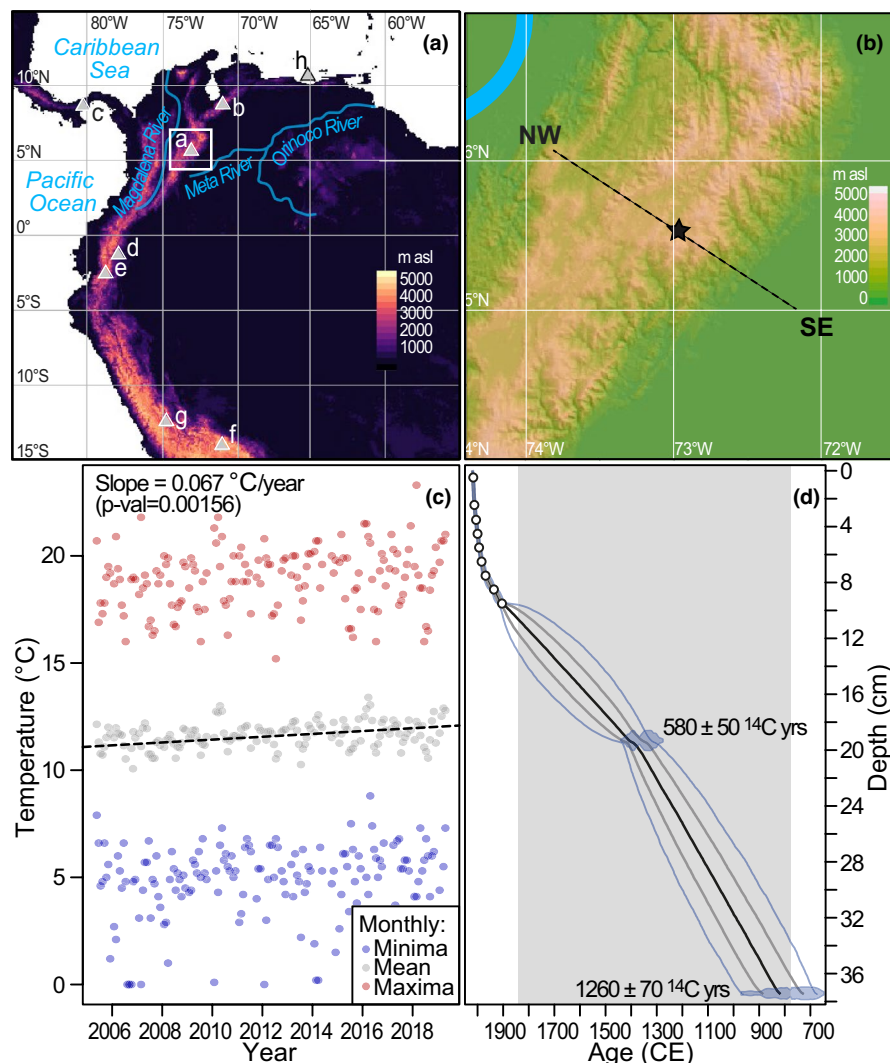
1.1 | Study area

Lake Tota (hereafter Tota) is located in the Eastern Cordillera of the Colombian Andes (5.54°N and 72.93°W) at 3017 meters above sea level (m asl). With an area of 55.1 km², the lake is elongated with a southwest-northeast orientation that measures ca. 16 × 6 km (Gibson et al., 2019) and relatively shallow platforms (<5 m) along the northern and eastern shores. The lake quickly deepens after a few 100 m offshore, reaching a maximum depth of ~62 m in the south-central portion of the lake basin. The western and southern shores have limited littoral areas that rapidly descend offshore to depths of 10s of meters. The lake receives meteoric inflows from its ca. 201 km² drainage basin that reaches elevations up to 3800 m asl. The basin is located on the divide between the Magdalena River and Orinoco catchments but drains east, ultimately contributing to the discharge of the latter through its tributary, the Meta River (Figure 1).

The local climate is characterized by mean annual temperature (MAT) and precipitation (MAP) of ~11°C and 1150 mm, respectively (Cañón & Valdes, 2011). Reflecting the steep regional environmental gradients, within 30 km around the lake, MAT and MAP vary by ca. 10°C and 1000 mm, respectively, showing a negative association with elevation (Figure 1). The high diversity of climates created by these environmental gradients results in high vegetation turnover in the catchment basin and surrounding areas, creating a rich mosaic of floras.

The natural vegetation in and around Tota's watershed is mainly represented by Andean forest, sub-paramo and paramo, with their altitudinal limits and spatial distribution mostly defined by the daily temperature cycle (Cuatrecasas, 1958; Rangel-Ch et al., 1997),

FIGURE 1 Study area. (a) The eastern cordillera of Colombia (white box) in the context of northern South America; other records seen in the figure: (a) Lake Tota, (b) Laguna Blanca (Polissar et al., 2006); (c) Lake San Carlos (Correa-Metrio et al., 2016); (d) bog of Papallacta (Ledru et al., 2013); (e) Lake Pallcacocha (Moy et al., 2002); (f) Quelccaya ice cap (Thompson et al., 2013); (g) Laguna Pumacocha (Bird et al., 2011); (h) Cariaco Basin (Haug et al., 2001). (b) the regional topographic context of Lake Tota (represented by a star), showing the environmental transect developed in Figure 5. (c) Monthly minima, mean and maxima temperatures recorded in Aquitania meteorological station, located at the eastern shore of the lake (5.56°N 72.88°W, data from <http://www.ideam.gov.co/>); a linear regression of temperature as a function of time shows a statistically significant warming of $\sim 0.067^{\circ}\text{C}/\text{year}$ ($p\text{-val}=0.00156$). (d) Age–depth model; ^{210}Pb dates are represented by white circles, whereas the calibration distribution of ^{14}C dates is represented by blue silhouettes (uncalibrated ^{14}C dates are shown beside their calibration distribution); the section analysed for proxies is highlighted in grey



which, in turn, is largely controlled by elevation. Andean forests dominate elevations of between 2500 and 3500 m asl, and are characterized by arboreal taxa such as *Clusia*, *Hedyosmum*, *Myrsine*, *Podocarpus*, *Quercus* and *Weinmannia* (Cuatrecasas, 1958; Rangel-Ch et al., 1997). The altitudinal distribution of these forests also depends on moisture availability, which is higher on the eastern flank of the cordillera that faces the eastern lowlands (Arias et al., 2021). Thus, whereas Andean forests reach elevations up to 3500 m asl on the eastern flank, their upper bound is lower towards the inter-Andean valleys where the rain shadow effect restricts them down to ~ 3200 m asl (Hooghiemstra et al., 2006; van der Hammen, 1974). Above the Andean forest, sub-paramo and paramo vegetation dominate the landscape (Cuatrecasas, 1958; Rangel-Ch et al., 1997). They consist of dwarf forests and open vegetation rich in Asteraceae, Ericaceae and Poaceae. The main difference between paramo and sub-paramo is the presence of shrubs in the latter, mainly represented by *Polylepis*, and other woody genera like as *Buddleja* and *Clethra* (Kessler, 2006). Although the transition from arboreal montane forests to grasslands is mostly a result of the physiological limitations imposed by freezing nocturnal temperatures, other factors such as human influence and the distribution pattern of species

across a given region have also played a significant role on this transition (Hooghiemstra et al., 2012). Across the region, microhabitats created by the rich topography together with the highly dynamic vegetation disturbance regime allow the persistence of taxa adapted to lower elevations, such as *Alchornea*, *Acalypha*, *Hieronyma*, *Sapium* and *Cecropia*, among others (Cuatrecasas, 1958; Gentry, 1993).

In terms of human occupation, Tota is in the Cundiboyacense altiplano, a high plateau largely coincident with the territory of the indigenous group that has inhabited the region since at least 500 BCE, known as the Muisca. The record of human occupation around Tota is rather scarce with most of the archaeological evidence coming from the more southerly highlands of the altiplano. Archaeological evidence of semi-permanent settlements for hunting has been reported for as early as 12,000 years before present (Correal Urrego & Van der Hammen, 1977; Herrera, 2008). A substantial increase in human population occurred between 400 BCE and 800 CE with the development of agriculture, commerce with other regions and permanent settlements (Broadbent, 1971; Langebaek, 1995). The interval from 800 to 1500 CE is divided into the early and late Muisca periods, the latter characterized by a consolidation of the permanent settlements, an increase

in population and the establishment of densely populated urban centres with a complex social structure (Boada, 2006; Broadbent, 1974). Although there is no certainty of the population size before the Conquest, between 1550 and 1600 CE, the indigenous populations of the region decreased ~75% as a result of disease and war (Francis, 2002).

2 | MATERIALS AND METHODS

2.1 | Core collection and depth–age model

Three sediment cores were collected from Tota using a Uwitec gravity coring system in June 2013. Core H-13 core was collected in ca. 35 m water depth and measured 45 cm in length. It was extruded in the field at 0.5 cm intervals from 0 to 8 cm and sampled in the laboratory at 1 cm intervals from 8 to 40 cm at the Indiana University-Purdue University, Indianapolis (IUPUI) Paleoclimatology and Sedimentology Laboratory. Accelerator mass spectrometry (AMS) radiocarbon (^{14}C) ages were determined for two samples from the Tota cores at the University of California, Irvine. All materials were comprised of charcoal fragments that were pre-treated using an acid–base–acid wash (1 N HCl and 1 N NaOH). AMS ^{14}C measurements were made at the University of California Irvine (UCI) Keck Carbon Cycle AMS Facility. AMS ^{14}C ages were calibrated to common era and before common era years (CE/BCE) using the IntCal20 calibration curve (Reimer et al., 2020). ^{210}Pb , ^{210}Po and ^{137}Cs were measured on the H-13 core from 0 to 13.5 cm with ages calculated using the constant rate of supply (CRS) method (Appleby & Oldfield, 1978). 1000 age model iterations for the Tota record were produced using Bchron (version 4.1.2, compiled in R) (Haslett & Parnell, 2008), which accounts for both calibration uncertainty in ^{14}C data and potential changes in accumulation rates of the archive. The age model was assembled according to the empirical distribution of iterated age models, calculating the corresponding 2σ uncertainty ranges for each depth.

2.2 | Sediment analysis

Twenty samples spread along the 40-cm sediment core were analysed for palynological content. Samples were prepared according to standard protocols (Faegri & Iversen, 1989). Pollen counts were carried out under transmitted light microscope at x400 and x1000 magnifications, aiming at a pollen count of 250 grains per sample. Pollen taxa were identified using publications on regional pollen (Hooghiemstra, 1984; Velasquez, 1999) and the modern reference collection of the Smithsonian Research Tropical Institute. Sediment was subsampled every cm for geochemical analysis. Samples were dried and crushed with a mortar and pestle. Geochemical analyses, including total carbon (TOC), total inorganic carbon (TIC), total nitrogen (TN), $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ on bulk organic matter, were performed

at the Light Stable Isotope Mass Spectrometer Laboratory in the Department of Geological Sciences at the University of Florida (details in Appendix S1).

2.3 | Numerical analyses

A non-metric multidimensional scaling (NMDS) was performed on the palynological dataset to represent it in two dimensions (Legendre & Legendre, 1998). The ordination was based on Bray–Curtis dissimilarities among pollen samples, using only taxa that were present in three or more samples. The new bi-dimensional space was interpreted in terms of MAT and MAP using loess regressions with a span of 0.75 (see Appendix S2, Cleveland & Devlin, 1988). The regression consisted of a response surface of the environmental variable as a function of NMDS scores so that environmental estimates can be made for each sample. The regressions were based on MAT and MAP optima for genus-level-identified taxa represented in the fossil pollen spectra. Such optima were derived from modern environmental distributions of taxa that were estimated using geolocated occurrences of each taxon in the BIEN database (Maitner et al., 2018), and subsequently using geographical coordinates for extracting MAT and MAP from the WorldClim global database (Fick & Hijmans, 2017). The extracted climatic data for each taxon were summarized through a bivariate probability density function (PDF) (Wand & Jones, 1994) with density values above the 0.95 quantile representing taxon's modern optimum MAT and MAP. Climate estimates were then based on predicted MAT and MAP for sample scores based on the selected model. Lastly, a three-sample moving average was applied to the climate estimates to eliminate high-frequency noise.

Regional rasters of MAT and MAP, and the PDFs of each taxa were used to estimate the probability density of each taxon at each point across the modern geographical space. The resulting maps represent the modern environmental fitness of each taxon across the region, defined as its degree of affinity for specific combinations of MAT and MAP. These environmental fitness maps were used to contextualize the vegetation changes revealed by the pollen sequence into the modern spatial environmental variability.

Modern rate of temperature change was estimated based on instrumental monthly data from Aquitania meteorological station (data from <http://www.ideam.gov.co/>), covering from 2005 to 2019. For this purpose, we ran a linear regression model of mean monthly temperature as a function of time in years. The slope of the regression was used for constructing statistical hypotheses for comparing past rates of temperature change through t tests (Zar, 1999). Past rates of change were calculated using estimated temperature changes and time increments between contiguous fossil samples. Modern rates of temperature change were summarized using a Normal distribution (Zar, 1999), using the slope and standard error as μ and σ , whereas past rates of changes were summarized through nonparametric probability density functions (Silverman, 1986).

3 | RESULTS

The section analysed covered from ~800 to 1850 CE. The mean pollen sum per slide was 280 grains, except for the two basal samples which had pollen counts below 100 grains. A total of 82 palynological morphotypes were identified among the 18 samples that contained sufficient pollen (Figure 2). Pollen types were represented by 42 genera and 33 families, whereas spores were represented by five morphotypes, including *Selaginella* and *Isöetes* (Figure 2). In all, 12 taxa were present through the entire record, whereas 27 taxa were in fewer than two samples. The number of taxa per sample varied between 25 and 37, with the first and third quartiles in 30 and 34 taxa, respectively.

Although a progressive turnover of pollen assemblages was evident through the record (Figure 2), there was a substantial compositional change around 22 cm (~1250 CE). Below this depth, pollen assemblages were characterized by relatively high abundances of *Arecaceae*, *Cecropia*, *Borreria*, *Fabaceae*, *Melastomataceae*, *Myrsine*, *Piper* and *Poaceae*. Above 22 cm depth, the aforementioned taxa decreased while *Acalypha*, *Ambrosia*, *Brassicaceae*, *Gaiadendron*, *Plantago*, *Quercus*, *Solanaceae* and *Weinmannia* increased and persisted towards the top of the record. Around the middle part of the record, *Alchornea*, *Hedyosmum*, *Juglans*, *Myrica* and *Podocarpus* became relatively abundant.

From ~800 to 1400 CE, pollen of arboreal taxa increased from ~21 to ~33%, and then decreased to ~16% at ~1850 CE (Figure 3a). Similarly, pollen from herbaceous taxa progressively decreased through the record, reaching maximum and minimum values of 44 and 16% at ~850 and 1400 CE, respectively. In contrast, aquatic pollen taxa (Figure 3g) and spores from pteridophytes progressively increased through the record (Figure 3c). The carbon and nitrogen content and their isotopic ratios showed patterns of variability like those shown by the pollen record. Concentrations of TC, TOC and TN that indicate organic matter in the sediment were relatively high from ~800 up to ~1120 CE, showing a decreasing trend from this point towards the top of the record (Figure 3i–k). C/N ratios, which reflect the dominant source of organic matter, showed stable values of ~11 from the bottom of the record up to ~1250 CE, and decreased moving upward from this point (Figure 3l). Values of $\delta^{13}\text{C}$, associated with changes in organic matter contributed by vegetation types, became progressively more negative through time, going from -20.89 ‰ in the bottom to -23.14 in the top (Figure 3f).

The NMDS was run using 46 taxa that met the criterion of being represented in at least three samples, excluding aquatics. A convergent solution of the NMDS (stress = 0.22) was reached after 20 iterations (Figure 4a,b). Taxon ordination scores along NMDS1 and NMDS2 varied between -0.750 and 0.508, and -0.489 and 0.671,

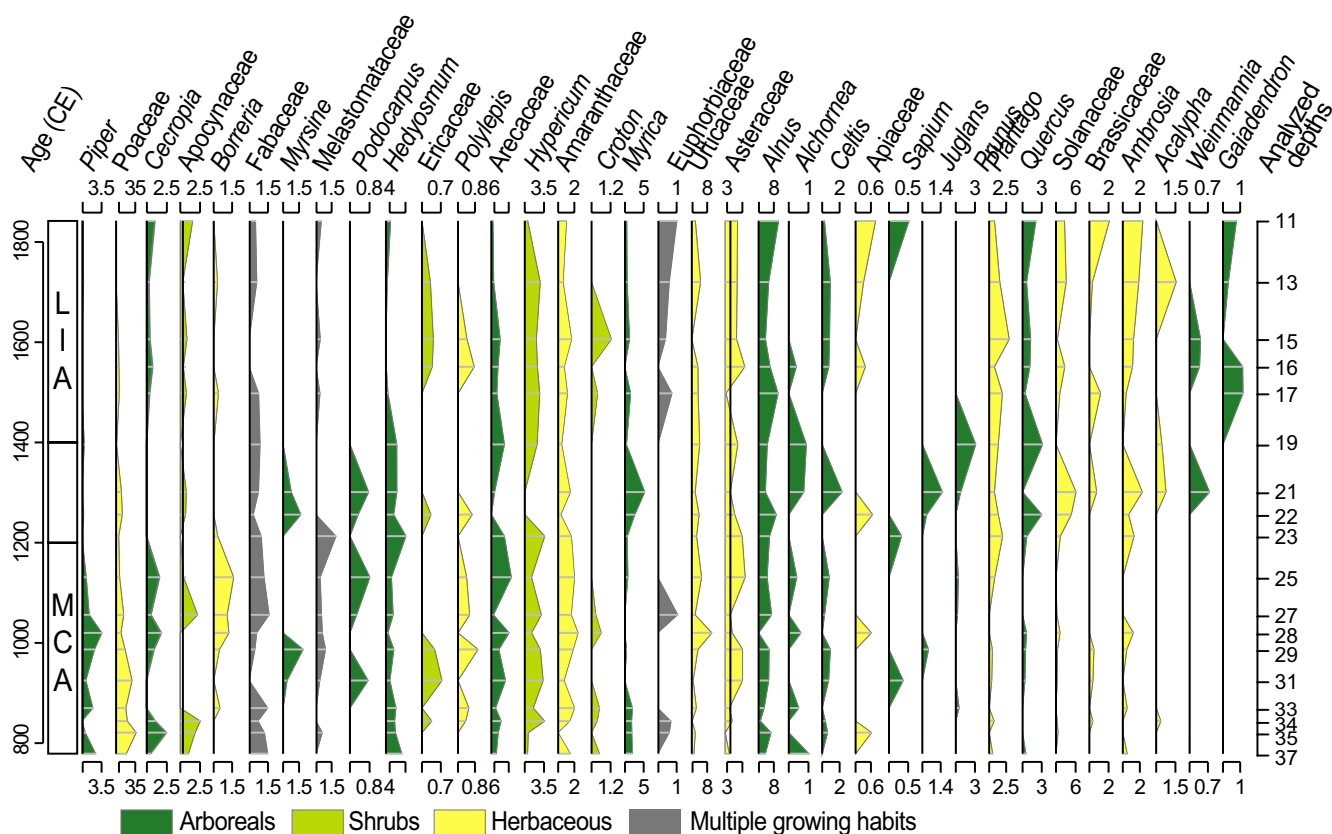


FIGURE 2 The palynological record of Lake Tota plotted against age and depth. Whereas time is represented along the y-axis, silhouettes show changes of relative abundance for each taxon. Only taxa that were used for the environmental reconstruction and those present in more than five samples are shown. The sequence of taxa from left to right is according to averages of time weighted by taxon abundance in each sample

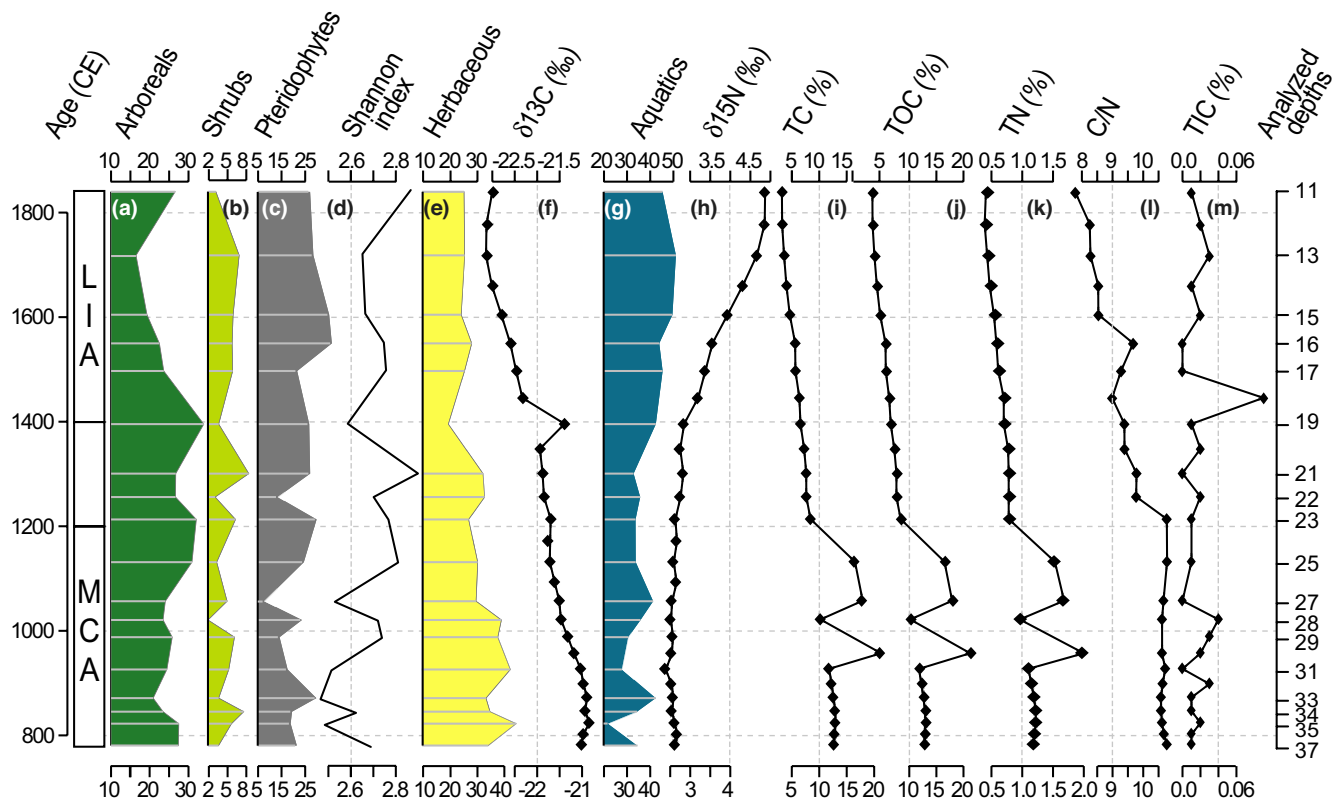


FIGURE 3 The sedimentological record of Lake Tota. (a–c), (e) and (g). Summary of pollen and spores assemblages grouped by vegetation growing habits (growing habits after Gentry, 1993; Marchant et al., 2002). (d) Shannon index of pollen assemblages. (f) and (h). Organic matter $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. (i–m). Carbon and nitrogen content in the sediments. Grey dashed lines are referential for age (horizontal) and geochemical values (vertical)

respectively. Sample scores varied from -0.484 to 0.389 along NMDS1, and between -0.340 and 0.341 along NMDS2. From within the 46 taxa used for the NMDS, 23 were identified at genus level, and therefore, their environmental envelope, represented by a bivariate PDF, was estimated (Appendix S3). According to the PDFs, conditions that maximized the probability density of taxon occurrence (0.95 quantile) were characterized by MATs from 4.6 to 24.2°C (first and third quartiles between 11.9 and 21.0°C) and MAPs from 253 to 2367 mm/yr (first and third quartiles between 1085 and 1463 mm).

Samples were ordinated within the space defined by the taxa identified at genus level, and thus, it was possible to estimate MAT and MAP for each sample using the loess model (Figures 4 and 5). Reconstructed temperatures were between 16.5 and 18.6°C between ~ 780 and 1050 CE , progressively decreasing down to $\sim 12^\circ\text{C}$, a mean temperature that characterized the time period from ~ 1500 to 1750 CE (Figure 5e). Reconstructed precipitation was characterized by values between 1000 and 1200 mm , with a marked increase up to 1400 mm between 1200 and 1400 CE (Figure 5g).

The linear regression used to describe the modern temperature trend was statistically significant (F-statistic = 5.925 ; d.f. = $[1, 154]$; p -value = 0.01607), with a slope of 0.067°C/year (s.e. = 0.027 , $t = 2.434$, p -value = 0.0161). Rates of temperature change of the past varied between -0.31 and 0.027°C/year , with a mean of -0.005 , and were statistically lower than modern warming rates (H_0 :

$\mu \geq 0.067$; H_A : $\mu < 0.067$, $t = -15.32$, p -value = 1.92×10^{-10}). The mean of absolute values of past rates of temperature change was 0.015 , also significantly lower than modern warming rates (H_0 : $\mu \geq 0.067$; H_A : $\mu < 0.067$, $t = -18.71$, p -value = 1.32×10^{-11}).

4 | DISCUSSION

4.1 | Vegetation turnover

From ~ 780 to $\sim 1300\text{ CE}$, the high abundance of herbaceous taxa (Figure 3e), especially Poaceae and Amaranthaceae (Figure 2), suggests relatively open vegetation at and around Tota. The dominance of herbaceous taxa, together with rather thermophilous elements such as Fabaceae and Arecaceae (Figure 2), indicates generally warm conditions. Today, only a few genera of the Arecaceae family are distributed in the high Andes (e.g., *Ceroxylon*, *Parajubaea* and *Wettinnia*), reaching altitudes as high as 3500 m asl (Borchsenius & Moraes, 2006; Gentry, 1993). Warmer conditions through this time period are also indicated by relatively high percentages of *Cecropia*, *Borreria*, *Hedysomum*, *Melastomataceae* and *Piper*, elements that, today, are mostly distributed through sub-Andean forests at elevations below 2500 m asl (Cuatrecasas, 1958; Rangel-Ch et al., 1997). Concurrent high abundances of herbaceous taxa associated with

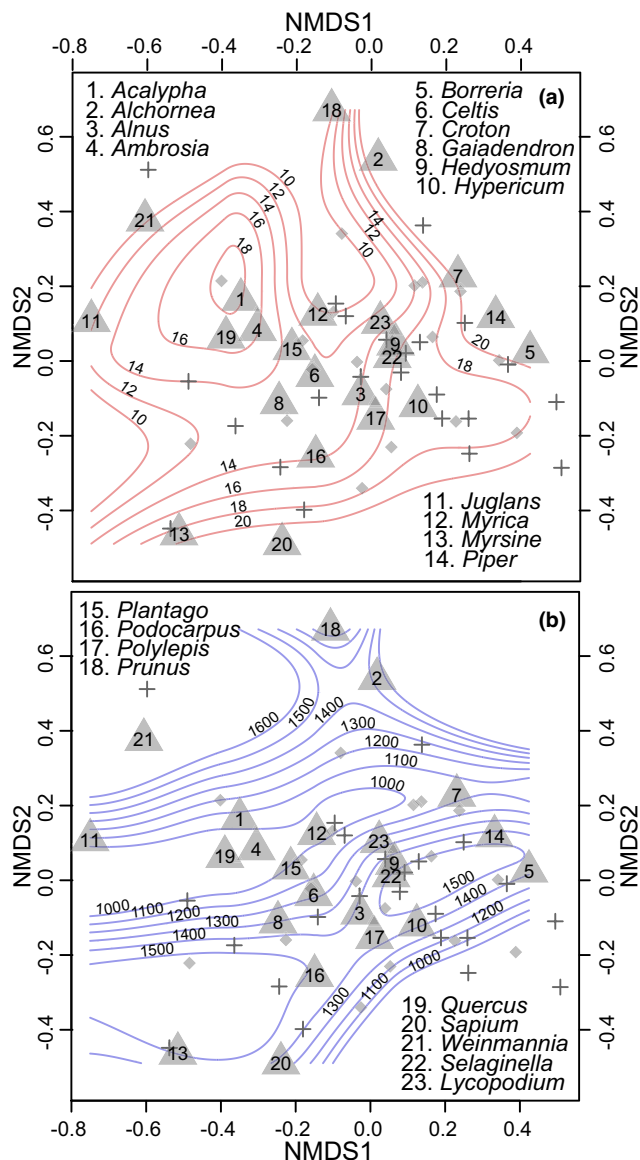


FIGURE 4 Non-metric multidimensional scaling of the palynological sequence of Lake Tota. (a) and (b); ordination of taxa (triangles and crosses) and samples (diamonds) with mean annual temperature isolines (a) and mean annual precipitation (b) based on optima estimated for taxa represented by triangles. See Appendix S2 for details on estimation of isolines

dry conditions and arboreal elements associated with warmer conditions indicate relatively high climate seasonality. Dry conditions with highly seasonal precipitation have also been reported for other low-latitude areas during this time interval (e.g., the Peruvian Andes, Bird et al., 2011; the Central Cordillera of Panama, Correa-Metrio et al., 2016; and the Venezuelan Andes Polissar et al., 2006), in apparent coincidence with the Medieval Climate Anomaly (MCA) for the northern neotropics.

Taxa that dominated the pollen spectra through the MCA are today associated with environments that lie some 20 km from Tota and at elevations around 2500 m asl or less (Figure 5c). These areas are predominantly located on the eastern side of the eastern Andean

Cordillera that descends into the Orinoco Basin and more rarely across the western flank that drains towards the inter-Andean valley of the Magdalena River (Figure 5c). Given the warmer conditions that characterize the MCA (Mann et al., 2009), these taxa are likely to have migrated upslope from both flanks. This scenario is plausible, as upslope migration rates of up to 3.5 vertical meters per year have been documented for tree genera in the Peruvian Andes under modern warming conditions (Feeley et al., 2011). Nevertheless, the temperature estimates for the MCA are probably amplified by the over-representation of upslope wind transported taxa commonly found in the Andes (Grabandt, 1980). Furthermore, convective transport of heat up the Andean flanks was probably strengthened by higher temperatures, reinforcing upslope transport of pollen, as has been suggested for other regions of the equatorial Andes (e.g., Bog of Papallacta, Ecuadorian Andes, Ledru et al., 2013).

During the transition from the MCA to the LIA, from ~1250 to ~1350 CE, a shift to moister conditions is suggested by a reduction of herbs, and a substantial increase in arboreal taxa (Figures 2 and 3a,e). Thermophilous taxa that were common in the bottom of the record were replaced by montane and upper montane taxa, mainly represented by *Myrsine*, *Podocarpus*, *Myrica*, *Alchornea* and *Prunus* (Figure 2). While moisture availability increased, this transition was accompanied by a marked reduction in temperature. Overall, pollen assemblages between ~1250 and ~1350 CE reflect a highly diverse vegetation with elements from a broad range of elevations and forest types producing the highest values of Shannon index through the record (Figure 3d). It is likely that the transitional climate (warm and dry to cold and wet) was associated with an ecosystem without modern analogue that resulted from the coexistence of early arrivals of taxa that would dominate during the LIA and lagging floristic elements from the assemblages that dominated earlier during the MCA (Williams & Jackson, 2007). In the modern landscape, environments with the potential for harbouring these rich assemblages (high fitness for most of the taxa found in the fossil record) lie some 25 and 60 km towards the eastern and western flanks of the Cordillera, respectively (Figure 5).

The decrease in arboreal elements and a slight increase in shrubs from ~1400 CE to the top of the record at 1850 CE (Figure 3a,b) suggests a stronger influence of sub-paramo vegetation (Cuatrecasas, 1958; Rangel-Ch et al., 1997). This finding is consistent with local cooling in response to widespread Northern Hemisphere cooling that took place during the LIA (Mann et al., 2009). Increases and persistence of *Gaiadendron*, *Plantago*, *Quercus*, *Weinmannia* and *Acalypha* suggest the establishment of a well-structured Andean forest, that today occurs at altitudes between ~2500 and 3500 m asl (Hooghiemstra et al., 2006). Along the inter-Andean flank of the Cordillera, moisture availability is lower because of the rain shadow and, thus, the forest line is lower on this flank. These drier conditions are well reflected by high percentages of herbaceous taxa in the record, mainly represented by *Asteraceae* and *Ambrosia* (Figure 2). Taxa that characterized the LIA in Tota show a high probability of modern occurrence towards the NW end of the analysed environmental gradient (Figure 5c), reflecting the stronger biogeographical

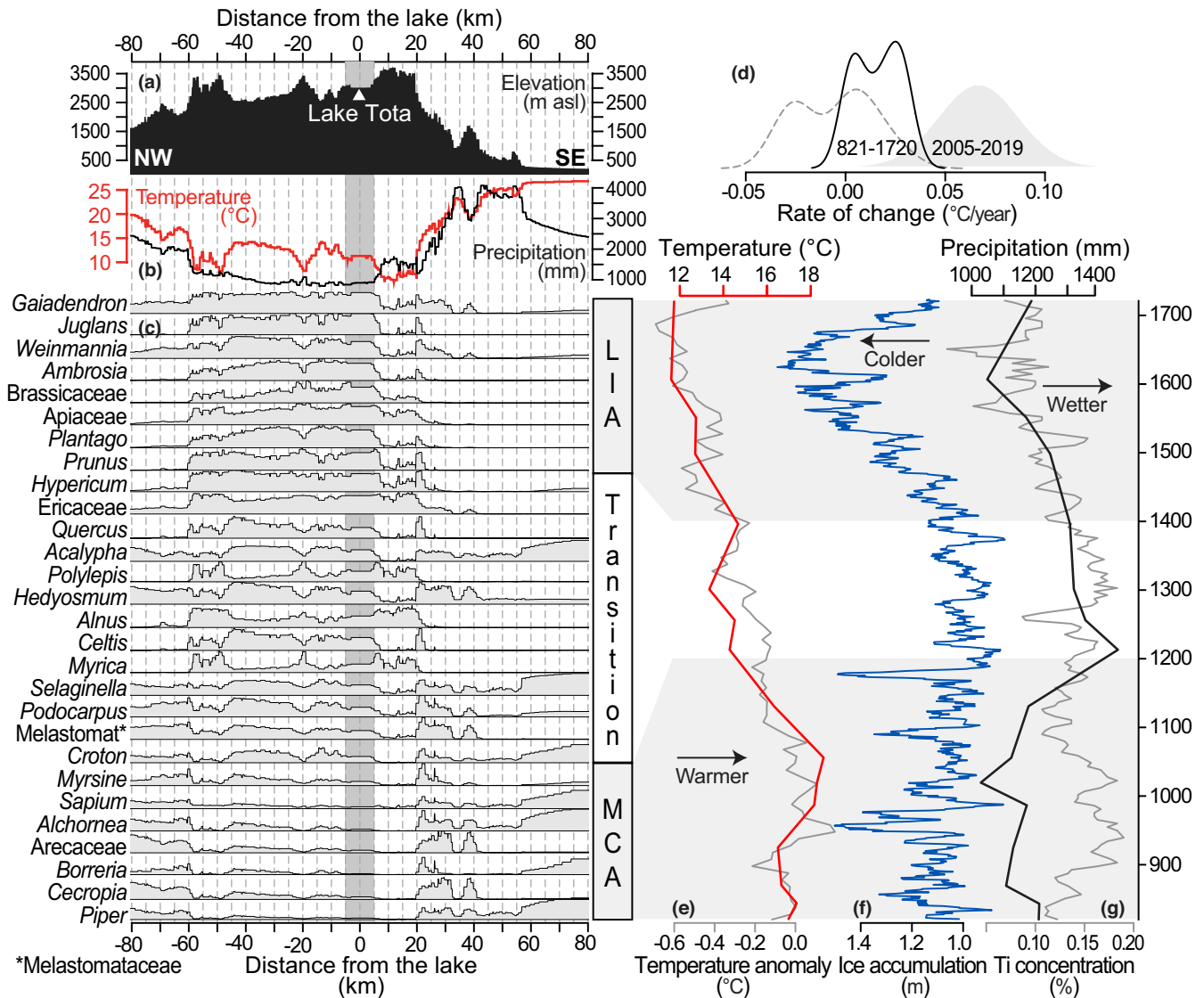


FIGURE 5 Climatic reconstruction based on the sedimentary record of Lake Tota in the context of modern regional environmental variability and ecological fitness of taxa. (a) and (b), elevation and mean annual temperature (red line) and precipitation (black line) profiles along the NW-SE transect shown in Figure 1. (c) Profiles of environmental fitness of selected taxa from the palynological record of Tota along the NW-SE transect shown in Figure 1; from bottom to top, taxa are ordered according to increasing environmental fitness under the modern climate of Tota; the right bar shows the main association of taxa with the environmental stages (combinations of MAT and MAP) evidenced by the sedimentary record; environmental data from Fick and Hijmans (2017). (d) Probability density functions of past (~800–1700 AD) and modern (2005–2019 AD) rates of temperature change: Past rates of temperature change in the dashed line, absolute value of past rates of temperature change in the solid line and modern rates of temperature change in the grey polygon. (e) Reconstructed (red) and global temperatures (grey) (Ljungqvist et al., 2012) during the studied time interval. (f) Ice accumulation on the Quelccaya ice cap Peruvian Andes (Thompson et al., 2013). (g) Reconstructed precipitation (black) and Ti concentration in the Cariaco Basin (grey) (Haug et al., 2001)

influence of the inter-Andean valley on vegetation composition during this time interval.

Changes in human occupation usually produce changes of vegetation. The vegetation turnover revealed by our record, however, does not coincide with the human population changes reported for the area. Whereas substantial vegetation changes are evident in our record since at least 1200 CE (Figure 2), the most important change of human population in the region was the decline that took place between 1550 and 1600 CE (Francis, 2002). Furthermore, changes of taxa that usually associate with human occupation do not show

synchronicity. For instance, *Cecropia* and *Poaceae* are abundant from ~800 to 1200 CE, *Ambrosia* is abundant from ~1200 to 1800 CE, and *Asteraceae* and *Amaranthaceae* characterize the entire record (Figure 2). At the community level, however, the increased forest cover coincides with that reported for other regions of the tropical Andes and the Amazon, where forest regrowth occurred after the MCA, possibly reflecting reduced human activity in the landscape long before European arrival (e.g., Åkesson et al., 2020; Bush et al., 2021). Thus, besides climatic drivers, our pollen record probably reflects a long-term trend of land use by people. Nevertheless, a



longer record would be necessary to provide the adequate context for regional human occupation during the mid- and late Holocene.

4.2 | Environmental turnover

The total carbon content of the sediments of Lake Tota is mostly composed of organic carbon, with the inorganic fraction representing on average 0.24% of the sediment (Figure 3i). Thus, through the studied time interval, the carbon dynamics of the lake were dominated by biological processes. Although the absolute range of the $\delta^{13}\text{C}$ record is just 2.3 ‰, the trend towards more negative values from 900 CE to present (Figure 3f) indicates a progressive decrease in the contribution of grasses to the bulk organic matter accumulated in the sediments (Meyers, 2003). This observation further supports the inferred evolution of the regional vegetation from open canopies during the MCA towards more closed forest during the LIA. Indeed, relatively high C/N ratios from ~800 to 1200 CE (Figure 3l) indicate a higher contribution of terrestrial sources of the accumulated organic matter (Meyers, 2003), a probable result of a more erosive action from precipitation given a more open vegetation. This ratio gradually decreased from 1200 to 1800 CE, as a result of a progressively lower relative contribution of terrestrial sources to the accumulation of carbon in the sediments. Vegetation turnover suggests a progressive cooling, which, in turn, would have resulted in lower evaporation and, thus, in a progressively increasing lake level. Given the morphology of the lacustrine basin (Gibson et al., 2019), relatively shallow littoral regions developed as the lake level increased, resulting in the progressive increase of aquatic vegetation (Figure 3g). This ring of littoral vegetation probably acted as a trap for organic matter (carbon) eroded from the catchment basin, thus accounting for the decrease of TC and TN during the LIA. Furthermore, the sustained increase in $\delta^{15}\text{N}$ (Figure 3) could be related to the increasing lake level causing longer periods of anoxia in the bottom water and producing denitrification (Hodell & Schelske, 1998).

The accumulation of high probabilities of taxon occurrence across relatively narrow environmental areas indicates that MAT and MAP play an important role at defining taxon presence (Appendix S3). The high dispersion of the first probabilistic quartile was probably caused by taxon occurrences that are not directly associated with climate and the aggregation of pollen taxa at genus level. Most of the analysed taxa (19 of 23) showed a unimodal distribution, implying convergence of the environmental preferences of taxa from the same genus as has been reported at family level (Punyasena, 2008). *Gaidendron*, *Hedyosmum*, *Selaginella* and *Weinmannia* showed bimodal distributions that probably resulted from their wide distribution and/or the presence of multiple species in the region (Cuatrecasas, 1958; Rangel-Ch et al., 1997). The upper quartile (occurrence probabilities above 0.75) of the distribution of each taxon along the temperature gradient coincides with the altitudinal distribution of modern pollen in the Eastern and Central Cordillera of Colombia (Wille et al., 2001) and the southeastern Ecuadorian Andes (Niemann et al., 2010). Thus, vegetation and pollen distribution along the regional gradient

of MAT are comparable, supporting our approach of using environmental distributions derived from vegetation to interpret the fossil palynological record.

The trend of estimated temperatures closely follows global and Northern Hemisphere temperatures (Ljungqvist et al., 2012; Mann et al., 2009), as well as patterns of ice accumulation in the Peruvian Andes (Thompson et al., 2013) (Figure 5e,f). Temperatures of between 17 and 18°C for the MCA and around 12°C during the peak for the LIA represent a change of between 5 and 6 °C through a time interval of ~1000 years (Figure 5e). The amplitude of this change probably represents the regional differential between the maximum warming of the MCA and the minimum cooling of the LIA, as our record is truncated before global temperatures rebounded (Figure 5). The magnitude of the reconstructed MAT variation, however, is likely too high given the ~8 °C amplitude of the glacial-interglacial cycles reported for the region (Flantua et al., 2019; Groot et al., 2011). The influence of wind-transported lowland pollen probably exaggerated the temperature estimation through the entire record. During the MCA, temperature overestimations were probably larger than for the LIA given a more open regional vegetation associated with lower pollen productivity and enhanced convective activity along the Andean flanks. Also, it is possible that, although during the amplitude of global temperature change was ~1 °C (Mann et al., 2009), it was larger at higher elevations given feedback mechanisms associated with the cooling of the LIA (Ning et al., 2020). As temperatures decrease, cloud lines migrate downslope, causing more heat loss at higher elevations and, therefore, amplifying the cooling (Bush et al., 2007; Ning et al., 2020). Furthermore, under a scenario of higher human impact during the MCA than during the LIA, forest recovery would amplify the climatic signal (Bush et al., 2017), leading to an overestimation of climatic fluctuations. Lastly, it is important to notice that temperature estimations were based on fossil pollen and modern distribution of parental taxa, which, given that pollen-vegetation relationships are not one-to-one, could also be causing a bias towards exaggerated temperature variability. The relative changes in temperature between the MCA and LIA, however, are reflective of changing climatic conditions between these two prominent climate events.

Precipitation estimations followed a pattern of relatively dry conditions with a relatively wet interval between ~1100 and 1500 CE, largely coinciding with the MCA-LIA transition. Through the Holocene, precipitation in the Neotropics is suggested to have been related to the southward latitudinal migration of the Inter Tropical Convergence Zone (Haug et al., 2001). However, during most of the MCA, whereas the Cariaco record indicates relatively wet conditions in northern South America (Haug et al., 2001), the vegetation at Tota suggests relatively dry and seasonal conditions (Figure 5g). According to the sedimentary record of Lake Pallcacocha, Ecuadorian Andes (Moy et al., 2002, Figure 1), El Niño frequency intensified during this time interval, providing a plausible explanation for the dry conditions in Tota as, in the region, this phenomenon is associated with a generalized decrease in annual precipitation (Poveda et al., 2011). Additionally, warmer MAT around Tota and

increased atmospheric convection along the flanks of the cordillera could have increased low elevation rainout, resulting in reduced moisture delivery to higher elevations (Bird et al., 2018). Similar climatic conditions have been reported for other neighbouring areas during this time interval (e.g., Laguna Pumacocha, Peruvian Andes, Bird et al., 2011; Lake San Carlos, Central Cordillera of Panama, Correa-Metrio et al., 2016; Laguna Blanca, Venezuelan Andes, Polissar et al., 2006), providing support to our interpretation. During the MCA-LIA transition, our precipitation reconstruction shows an in-phase pattern with the Ti record of Cariaco Basin from ~1100 to 1700 CE (Figure 5g), suggesting a precipitation increase that has been reported for other areas of the Ecuadorian and Peruvian Andes (e.g., Apaéstegui et al., 2014; Ledru et al., 2013). During the LIA, precipitation appears to have returned to levels like those of the MCA. However, the pressure on vegetation was probably ameliorated by colder temperatures that resulted in much lower evapotranspiration and, thus, higher overall effective moisture.

4.3 | Past and modern rates of temperature change

Methodological limitations inherent to both palynological and statistical analyses and the probable amplification of the climatic signal by human influence resulted in a record that apparently exaggerated temperature changes. However, the general trend of the temperature reconstruction is coherent with the independent geochemical indicators of our record (Figure 3). More important, the resemblance of the estimated patterns of changes with global and regional records and the coherence between the observed past vegetation changes with the modern distribution of taxa offer compelling evidence for interpreting the environmental estimates in terms of regional trends (Figure 5e–g). At a regional scale, pollen–environment relationships are systematic, reinforcing the reliability of the trends shown by our reconstruction (Grabandt, 1980; Groot et al., 2011; Weng et al., 2007). According to monthly temperature data from Aquitania meteorological station, located in the eastern edge of Lake Tota, during the last 16 years, there has been a progressive warming of $\sim 0.067^{\circ}\text{C}/\text{year}$ (Figure 1c). Previous studies have reported a progressive regional increase of relative humidity (Poveda, 2004), which could be associated with increases in evapotranspiration associated with the temperature rise. The warming rate of the last 16 years is unprecedented within the time frame encompassed by our record (Figure 5), even considering the fact that our estimates overstate the amplitude of the temperature change that took place between the MCA and the LIA. Rates of past temperature change were significantly lower than the modern warming rate. Indeed, when past rates of change are considered as absolute values, the modern rate of warming is more than four times higher than that of the past ($\sim 0.015^{\circ}\text{C}/\text{year}$).

According to the pollen record of Lake Tota (Figure 2), the regional vegetation turnover that occurred between the LIA and MCA was rather broad. Our analysis of modern environmental affinities of

taxa in space shows that a similar pattern is expressed today across an area defined by a radius of ~ 30 km around the centre of the lake (Figure 5c). Steep altitudinal gradients probably played a fundamental role for such large temporal vegetation turnover to take place (Bush, 2002). Given that modern rates of temperature change have no precedent within the last 2000 years, modern vertical migration rates of ~ 3.5 m/year (Feeley et al., 2011) are probably higher than those that took place through the studied time interval. Thus, migration alone would be insufficient for explaining the vegetation changes evidenced by the palynological record. This observation highlights the importance of the physiographic diversity of the landscape that promotes the existence of microrefugia at maintaining natural ecosystems on the light of high environmental variability and rapid modern climate change.

5 | CONCLUSIONS

Between ~ 800 and 1800 CE, substantial environmental and ecological turnover occurred in the catchment of Lake Tota. According to the evidence offered by our sedimentary record, temperatures at Tota during this time interval were closely associated with the anomalies reported for other regions of the Neotropics, with warm and cold conditions during the MCA and the LIA, respectively. Precipitation patterns, on the other hand, were decoupled from the hemispheric trend during the MCA, when dry conditions persisted in Tota. Vegetation was highly dynamic through the studied time interval, with fast responses to climatic variability probably mediated by the steep environmental gradients of the region. According to our analysis of modern distribution of taxa, environmental conditions favourable to the taxa that marked the vegetation turnover between the MCA and the LIA in the catchment basin of Tota, can be found today within 30 km of the lake, towards the flank of the Cordillera that descends into the Orinoco basin. The wide variety of environmental conditions across this flank of the Cordillera promotes the coexistence of taxa whose cooccurrence would not be possible under uniform environmental conditions across the region. Thus, given the evidence provided by our palynological record, the upper elevations at the southeastern side of Lake Tota should be prioritized for conservation under the modern scenario of climate change. Although the amplitude of the temperature change at Lake Tota is likely overestimated by our approach, modern temperature change rates are unprecedented within the millennia we analysed. Our results provide substantive insight into understanding the effects of climate change on regional vegetation turnover in the high Andes, pointing at environmental heterogeneity as a key point for diversity conservation under scenarios of rapid climate change.

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DATA AVAILABILITY STATEMENT

Palynological data supporting this study are available through the Dryad repository (<https://datadryad.org/stash/dataset/doi:10.5061/dryad.hx3ffbggd>).

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**BIOSKETCH**

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Author contributions: JE, BWB and AC-M conceived the study. AC-M conducted the formal data analyses and led the writing of the manuscript. BWB, JE and BS retrieved the core. JE, BWB, DC-R, BS, PR-Z and JC produced the data.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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