Piazzentian Environmental Change and the Onset of Cool and Dry Conditions in Tropical South America

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Abstract The Piazzentian (3.60–2.58 Ma) covers the last stage of the Neogene just before the Earth’s climate turned from relatively stable warm conditions to the cooler climate with high amplitude glacial-interglacial oscillations of the Pleistocene. Even during this period early fluctuations towards cooler conditions occurred, and sea surface temperature (SST) reconstructions show stepwise increasing gradients. The zonal Pacific SST gradient which indicates the strength of the Walker circulation appears to have increased in two steps starting in the Piazzentian. We investigated vegetation and climate change in western equatorial South America under the influence of the Walker circulation and to detect signs for the onset of cooling in the tropics. We studied vegetation changes in western Ecuador using palynological analysis of 88 sediment samples from marine Ocean Drilling Program Site 1239 dated between 3.9 and 2.7 Ma. A general trend towards more open vegetation is observed. The climate changes towards cooler conditions, which is manifested by a lowering of the forest line from 3.3 Ma on. The increase of Amaranthaceae pollen after 3.1 Ma suggests drier conditions along the coast. A comparison with mid-Piazzentian warm period (mPWP) modeling shows that data and models agree regarding a drier coastal climate during the mPWP. The isochronous occurrence of environmental changes in the presented record, that is, cooling and coastal drying, with the first major pulse of ice-rafted debris and cooling temperatures in the Northern Hemisphere (between 3.28 and 3.31 Ma) suggests that these changes might have been a precursor of the intensification of the Northern Hemisphere glaciation.

Plain Language Summary Around 3.6 to 2.6 million years ago was a time in Earth’s history when many conditions were similar to today like the arrangement of the continents, vegetation, and greenhouse gas concentrations. However, the Arctic was not yet covered by ice sheets, and the global climate was warmer, making this time period well suited to study the drivers and mechanisms of warm climates. Towards the end of this period, global climate started to cool, which is known mainly from Northern Hemisphere climate reconstructions. We wanted to find out if cooling and drying conditions found in other records also occurred in the South American tropics. Fossil pollen assemblages preserved in marine sediments can tell us which plants grew in our study area (broadly western Ecuador). Since plants have different (known) climatic requirements, we can reconstruct past rainfall and temperatures as well. We find cooling and drying of neotropical climate, possibly linked to the period preceding the intensification of the Northern Hemisphere glaciation. Studying past climates can help us to better understand and constrain present and future climate developments.

1. Introduction

Warm climate states in Earth’s history are the target of many studies due to their potential to serve as an analogue for future climate change. The Piazzentian (3.60–2.58 Ma) is of particular interest because it is the most recent period of sustained warmth when most geological boundary conditions were similar to today, including the configuration of the continents, atmospheric CO₂ concentration, and flora and fauna (Dowsett et al., 1996; Haywood et al., 2016). Piazzentian mean global temperatures were substantially higher than pre-industrial temperatures. While the tropics were similar to today, high-latitude air temperatures were ~7°C warmer at 70°S and ~10°C warmer at 80°N (Contoux et al., 2012; Rickaby & Halloran, 2005). As early as 3.6 Ma, a gradual increase in mean global ice volume began leading ultimately to the Northern Hemisphere glaciation (Mudelsee & Raymo, 2005).

The climate in western tropical South America is strongly influenced by sea surface temperatures (SSTs) of the Pacific and the central Pacific SST gradient. SST records show a development of the eastern equatorial...
Paciﬁc (EEP) cold tongue at least as early as 3.6–3.5 Ma (Lawrence et al., 2006; Steph et al., 2010). Between ~3.6 and 3.2 Ma, the zonal SST gradient between the western Paciﬁc warm pool and the EEP cold tongue markedly increased (between Ocean Drilling Program [ODP] Site 806 and ODP Site 846; Figure 1). After 3.2 Ma, eastern and western Paciﬁc SSTs approached each other again until ~2.3 Ma (Fedorov et al., 2015). The increased zonal SST gradient would have strengthened the Walker circulation implying that during the (early) Pliocene a weaker Walker circulation resulted in more and stronger El Niño conditions (Wara et al., 2005), a state also called El Padre (Ford et al., 2015). A strengthened Walker circulation would become manifest in western Ecuadorean climate not only in the decadal variability but also in the long-term changes. Less precipitation over western Ecuador is expected when the strengthening of the Walker circulation causes the average latitudinal position of the intertropical convergence zone (ITCZ) to shift northwards (Perez-Angel & Molnar, 2017). At 2.6 Ma also the meridional SST gradient increased with the intensiﬁcation of the Northern Hemisphere ice sheets (Brierley et al., 2009; Figure 1).

A need for paleoclimate and paleovegetation records especially from South America of the mid-Piacenzian has been indicated by the PRISM4 group (Dowsett et al., 2016) to improve global vegetation reconstructions. The mid-Piacenzian warm period (mPWP) is a target modeling interval for understanding mechanisms and feedbacks that sustained such a warm climate. Several studies are available, modeling mPWP climate (Contoux et al., 2012), the atmospheric Hadley and Walker circulations (Kamae et al., 2011), and the orbitally forced interglacial climate variability and vegetation response (Prescott et al., 2014, 2018). While several

Figure 1. (a) Paciﬁc sea surface temperature reconstructions from 4.5 to 1 Ma (Brierley et al., 2009; Etourneau et al., 2010; Lawrence et al., 2006; Wara et al., 2005). Long-term trends are displayed as 400-ka running means for ODP sites 846, 1239 (study site of this study), and 1012, and as 600-ka running mean for ODP site 806, respectively. The zonal gradient increased in two steps between 3.6 and 1.7 Ma (gray shading), and the meridional gradient increased from 3.5 to 2.5 Ma (black box). WPWP = western Paciﬁc warm pool, EEP CT = eastern equatorial Paciﬁc cold tongue. (b) Locations of ODP sites shown in panel a.
proxy records document vegetation change and gradual cooling of high‐latitude climate in the Northern Hemisphere after ~3.5 Ma (e. g. Andreev et al., 2014; Brigham‐Grette et al., 2013; Demske et al., 2002; Panitz et al., 2016), reconstructions of Pliocene vegetation and terrestrial climate in the low latitudes are rare (e. g. Dupont, 2006; Hooghiemstra & Ran, 1994; Vallé et al., 2014). Several pollen studies from Colombia exist for the mid‐Pliocene (Hooghiemstra, 1989; Hooghiemstra et al., 2006; Van der Hammen et al., 1973; Wijninga, 1996; Wijninga & Kuhry, 1990). However, these records cover mainly the Andes and not the lowlands, which also should be considered when inferring changes in atmospheric circulation. While precipitation is the critical climatic factor in the lowlands (Vuille et al., 2000), the altitudinal vegetation belts in the Andes are also strongly temperature dependent (Hooghiemstra & Ran, 1994). Therefore, a pollen record covering both the coastal areas and the mountains could provide new insights into vegetation and climatic changes in western equatorial South America.

Vegetation and climate in this region are strongly influenced by the heterogeneous Andean topography. The timing of uplift in the area, however, is not yet fully resolved. Geologic activity in the western Andean Cordillera of Ecuador occurred as early as late Miocene times (Spikings et al., 2005), but geomorphologic data suggest that surface uplift only started in the early Pliocene and did not cease until the Pleistocene (Coltorti & Ollier, 2000). Two recent palynological studies from the Ecuadorian and central Andes recorded pollen typical of high‐altitude páramo vegetation in late Miocene sediments, suggesting the presence of elevations above the upper forest line at least since that age (Grimmer et al., 2018; Hoorn et al., 2017).

Here, we present a new record of Piacenzian vegetation and climate changes in western equatorial South America based on palynological analysis of sediments from ODP Site 1239 in the EEP. The aims of this study are (1) to investigate floral and vegetation changes, (2) to infer climatic changes from the response of the vegetation, and (3) to assess if and how the onset of global cooling is manifested in the study area. We compared our results with published climate modeling of the mPWP.

1.1. Modern Vegetation

The study region comprises western equatorial South America from southern Colombia to northern Peru and from the Pacific coast to the western Andean Cordillera. In this mountainous area the vegetation is arranged in belts, from the lowland along the coast to the high‐altitude páramo (Van der Hammen, 1985). In the coastal lowlands, tropical moist or dry broadleaf forest is found depending on the amount of precipitation received in the area (Figure 2). Typical elements of the lowland vegetation are Arecales (e.g., Mauritia), Fabaceae, and Rubiaceae, complemented by Araceae and Piperaceae in the understory (Gentry, 1986). The moist broadleaf forest occupies most of the Andean Cordilleras up to an altitude of about 3,200 m where trees become sparse. In the lower montane forest, which is found between 1,000 and 2,300 m, Acalypha, Alchornea, and Cecropia are common genera. Frequent taxa of the upper montane forest (2,300 to 3,200 m) are Alnus, Hedyosmum, Ilex, Myrica, Podocarpus, and Weinmannia. The upper forest line may be composed of Asteraceae, Ericaceae, and Polylepis (Rosaceae). The high‐elevation areas above the upper forest line are covered by montane grasslands and shrublands called páramo (Figure 2a), which is typically formed by Poaceae and species of Espeletia (Asteraceae) among others (Van der Hammen, 1985). Knowledge of modern pollen‐vegetation relationships is helpful for the interpretation of fossil pollen records (Niemann et al., 2010). A recent pollen rain study from southwest Ecuador shows that lake sediment surface samples capture the regional vegetation, with anemophilous taxa such as Podocarpaceae being overrepresented (Hagemans et al., 2019). Caryophyllaceae and Puya are examples of taxa which are underrepresented in the pollen rain compared to their abundance in the vegetation. This study further confirms the usefulness of Hedyosmum and Podocarpaceae as indicators for upper montane forest (Hagemans et al., 2019).

1.2. Modern Climate and Ocean Circulation

Rainfall is the most important climate factor in the lowlands. The variability in precipitation also impacts the vegetation in the mountains, but the altitudinal vegetation zones are mainly defined by temperature. The mean annual temperature at 1,500 m is 20°C (with absolute minimum and maximum temperatures of 5°C and 30°C, respectively). At 3,000 m, the mean annual temperature drops to 8°C (with a range from −4°C to 22°C; Pourrut, 1995). The general precipitation pattern is determined by the seasonal position of the ITCZ. Its southernmost position on the western South American coast is at about 4°S. Accordingly, precipitation is low in the coastal area further south (Figure 2b). At the precipitation equator (3–5°N), the
Figure 2. Map of the study site. (a) Present day vegetation types of western equatorial South America (World Wildlife Fund [WWF], n.d.), elevation contours delimiting the lower boundaries of the upper montane forest at 2,300 m and the páramo at 3,200 m (U.S. Geological Survey’s Center for Earth Resources Observation and Science, 1996), river mouths of Ecuador’s largest rivers, catchment area marked with a dashed half circle indicates the potential pollen source area, bathymetry of the eastern equatorial Pacific and location of Ocean Drilling Program (ODP) Site 1239. (b) Precipitation regimes of western equatorial South America (modified after Bendix & Lauer, 1992), southernmost limit of the intertropical convergence zone (ITCZ) during austral summer (dotted line), and main ocean currents (modified after W. S. Kessler, 2006). CC = Colombia current, EUC = equatorial undercurrent, NC = Niño current, PC = Peru current, SEC = south equatorial current.
annual precipitation has two maxima in April and October and two minima in January and July. Away from the precipitation equator, the Northern Hemisphere type of precipitation has one long dry season between October and March, while the Southern Hemisphere type is bimodal with one long dry season from April to September and a shorter one during austral summer. However, this pattern is strongly modified along the Ecuadorean coast, where a unimodal pattern with one rainy season during austral summer and a dry season in winter prevails (Bendix & Lauer, 1992; Figure 2b). The climate in this region is influenced by the cold Peru Current being the northern extension of the Humboldt Current (Pourrut, 1995). In the northern coastal area, the dominating westerly winds transport warm air from the Pacific which is heated by the seasonal southward directed warm Niño current (Bendix & Lauer, 1992).

The north and south equatorial currents flow westward between 10°N and 25°N and 0°S and 20°S, respectively (Brown et al., 2001). This flow is driven by the trade winds and causes the piling up of warm waters in the western Pacific (Pourrut, 1995). These currents are counterbalanced by the north equatorial counter current flowing eastward between 4°N and 10°N and the weaker south equatorial counter current between 5°S and 10°S (Brown et al., 2001). For a more detailed description of the oceanographic setting of ODP Site 1239, please refer to Grimmer et al. (2018).

1.3. Sediment and Pollen Transport to ODP Site 1239

ODP Site 1239 is situated near the eastern crest of Carnegie Ridge (0°40.32′S, 82°4.86′W), ~120 km offshore Ecuador, at a water depth of 1,414 m (Shipboard Scientific Party, 2003). Because of the prevailing westerly winds in the study area, the main pollen fraction is presumably transported to the ocean by rivers rather than by wind. Eolian transport of terrigenous sediments has been shown to play a major role only south of 5°S (Saukel et al., 2011). Rincón-Martínez et al. (2010) showed that terrigenous sediment transport to ODP Site 1239 is increased during humid interglacials and is therefore controlled by continental rainfall. Fluvial transport of pollen to the ocean depends on precipitation which is generally high within the range of the ITCZ. Secondarily, transport within the ocean depends on the direction of ocean currents. Terrigenous sediment supply at ODP Site 1239 is sourced at the delta systems of the Guayas (southern Ecuador) and/or Esmeraldas and Cayapas river (northern Ecuador; Rincón-Martínez, 2013). These rivers or rather their tributaries originate in the western flanks of the western Andean Cordillera (U.S. Army Corps of Engineers, 1998). Their catchment area which is assumed to be the main pollen source area is depicted in Figure 2. Although most of the sediment is deposited in the Ecuador Trench after reaching the ocean, the eastern part of the Carnegie Ridge still receives a moderate load (Pazmiño Manrique, 2005).

The evolution of the catchment area towards its modern configuration is closely linked to Andean uplift. From the eastern Peruvian Andes it is known that Andean-Amazonian drainage patterns started to establish as early as late Cretaceous to early Paleocene times (Hurtado et al., 2018). If a similar uplift history is assumed for the Western Cordillera of Ecuador, the modern catchment area might have been in place long before Pliocene times.

2. Methods

For the interval between 253 and 139 mbsf (3.6 and 2.7 Ma), 84 sediment samples of 10 cm³ were taken at 137-cm intervals on average from ODP Hole 1239A (cores 28X5–16H2). Four additional samples were taken between 3.9 and 3.6 Ma. Processing of the samples was done according to standard analytical methods (Faegri & Iversen, 1989), including decalcification with HCl (~10%) and removal of silicates with HF (~40%). Two tablets of Lycopodium spores (batch no. 177745 containing 18,584 ± 829 spores per tablet) were added to each sample during decalcification for calculation of pollen concentrations (Stockmarr, 1971). After neutralization with KOH (40%) and washing, the samples were sieved in an ultrasonic bath over an 8-μm screen to remove smaller particles. Samples were mounted in glycerol, and a minimum of 130 pollen grains and spores (280 on average) were counted in each sample with a Zeiss Axioskop at 400× and 1,000× (oil immersion) magnification. Because of variable pollen and spore counts, most percentage curves have been plotted with 95% confidence intervals, which size depends on the calculation sum. The Neotropical Pollen Database (Bush & Weng, 2007) and related literature (Hooghiemstra, 1984; Murillo & Bless, 1974, 1978; Roubik & Moreno, 1991) were used for pollen identification. Pollen types were grouped according to their ecologic preferences (Flantua et al., 2014; Marchant et al., 2002). The zonation was based on constrained incremental sum-of-squares cluster analysis (CONISS) of the pollen percentage curves, applying the square root
Table 1
Identified Pollen and Spore Taxa in Marine ODP Core 1239

| Vegetation type       | Pollen taxa                                      | Spore taxa                          |
|-----------------------|--------------------------------------------------|-------------------------------------|
| Páramo                | Orthrosanthus, Polyplepis/Acaena, Puya, Ranunculus, Sisyrynchium, Valeriana triphylla T | Jamesonia/Eriosorus, Huperzia        |
| Upper montane forest (UMF) | Acanthaceae, Bocconia, Clethra, Daphnopsis, Dodonaea viscosa, Hedyosnum, Melastomataceae, Morella, Myrsine, Podocarpaceae | Elaphaglossum, Lophosoria quadriripinata, Grammitis, Hypolepis hostilis T |
| Lower montane forest (LMF) | Alchornea, Bocconia, Passiflora, Styloceras T, Urticaceae/Moraceae, Vernonia T | Ctenitis subincisa, Cyatheaceae excl. Cyathea horrida, Pteris grandifolia T, Pteris podophylla T, Thelypteris |
| Lowland rainforest (LR) | Cordia lanata T, Socratea, Wettinia              | Pitrygogramma-Pteris altissima T, Pitrygogramma, Polypodiaceae |
| Broad-range taxa      | Amaranthaceae, Ambrosia/Xanthium, Anacardiaceae T, Apocynaceae, Artemisia, Bomarea, Bromeliaceae, Calandrinia, Caryophyllaceae, Cyperaceae, Ericaceae, Euphorbiaceae T, Ilex, Ligililiforae (Asteraceae), Liliaceae, Malvaceae, Monnina, Myrtaceae, Nyctaginaceae, Poaceae, Polygonum (Persicaria T), Proteaceae, Rosaceae, Salacia, Thevetia, Tournefortia, Tubuliliforae (Asteraceae) | Anemia T, Anthoceros, Cystopteris-Hyopolepis, Hymenophyllum trichophyllum, Lycopodiaceae excl. Huperzua, Saccoloma elegans T, Schizaea pennula, Selaginella |

Note. Grouping was done according to their main ecological affinity (Flantua et al., 2014; Marchant et al., 2002). T = type. Pioneer taxa are printed in bold.

The initial age model of ODP Site 1239 was based on biostratigraphic information (Shipboard Scientific Party, 2003). It was improved by correlating the benthic stable isotope records from Site 1239 with those from nearby ODP Site 1241 by visual identification of isotope stages (Tiedemann et al., 2007). Because Site 1241 has an orbitally tuned age model, this procedure resulted in an indirectly orbitally tuned age model for Site 1239, spanning the interval from 5 to 2.7 Ma (Tiedemann et al., 2007). The stable isotope record of Site 1239 exhibits two gaps in the interval between 3.0 and 2.7 Ma. Therefore, the stratigraphic position of MIS G10 is unsure.

3. Results

Grouping of the identified pollen taxa according to their main ecological affinity resulted in five groups: páramo, upper montane forest, lower montane forest, lowland rainforest, and broad-range taxa (Table 1). Taxa with single occurrences were excluded from the interpretation. The temporal resolution of the record is 10.8 ka on average in the interval from 3.6 to 2.7 Ma. The pollen concentration in this interval ranges from 580 to 2,959 grains per cubic centimeters (average: 1364 grains per cubic centimeters). Most numerous are Podocarpaceae pollen grains with values between 9% and 47%. The cluster analysis performed on the relative abundances yielded a division into four pollen zones (PiaI–PiaIV; Figure 3) which are described in the following section.

3.1. Floristic and Vegetation Changes From 3.9 to 2.7 Ma

Pollen zone PiaI (15 samples; 256.30–235.86 mbsf; 3.65–3.41 Ma): The average pollen and spores concentration in this zone is 1,288 grains per cubic centimeters. Pollen percentages of broad-range taxa (Poaceae, Tubuliflorae, Amaranthaceae, Ericaceae, Cyperaceae, Artemisia) are on a low level (10% on average). The abundance of most lower montane forest pollen increases (the sum increases from ~7% to ~10%). The lowland rainforest taxa show a similar trend. Podocarpaceae pollen, dominating the upper montane forest taxa, has a relative abundance around 30%. From 3.9 Ma on, Grammitis spores (upper montane forest) occur in the record. From 3.5 Ma on, pollen of Sisyrynchium, Orthrosanthis (páramo), and Hymenophyllum (broad range)
appears in the record. *Puja* pollen appears as a new páramo genus from 3.75 Ma on. The representation of páramo is rather low in this interval (sum páramo pollen 2% on average; Figure 3).

Pollen zone PiaII (30 samples; 234.60–187.71 mbsf; 3.40–3.08 Ma): The pollen and spores concentration increases substantially and reaches its maximum at 3.13 Ma with 2,960 grains per cubic centimeters. Percentages of broad-range taxa increase compared to pollen zone PiaI (~16%; e.g., *Artemisia*, *Rosaceae*, and *Cyperaceae*). In this group, Caryophyllaceae pollen first appear in the record around 3.24 Ma. The representation of the lower montane forest maintains high (~10%, mainly due to *Vernonia*, *Cyatheaeeae*, and *Styloceras*). *Clethra* (upper montane forest) pollen disappears after ~3.1 Ma. The abundance of upper montane forest pollen declines slightly (from 36% to 32%) and the abundance of páramo increases slightly (from 2% to 3%) compared to pollen zone PiaI, while pollen percentages of pioneer plants like *Elaphoglossum*, *Poaceae*, *Asteraceae* (*Tubuli florae*, *Artemisia*), and *Ericaceae* also rise (from ~8% to ~11%; Figure 3).

Pollen zone PiaIII (31 samples; 186.77–147.46 mbsf; 3.07–2.76 Ma): The pollen and spores concentration is low throughout this interval (1,104 grains per cubic centimeters on average). The abundance of tree/shrub pollen further declines whereas the abundance of herbs/grass pollen and broad-range taxa (18% on average; e.g., *Artemisia*) increases. The relative abundance of lower montane forest pollen decreases slightly compared to pollen zone PiaII (from 10% to 8%). The abundances of upper montane forest and páramo pollen remain constant. Amaranthaceae pollen increases substantially in abundance (from 0.3% to 0.9% compared to PiaIII; Figure 4). Pollen of pioneer plants like *Elaphoglossum*, *Poaceae*, *Artemisia*, and *Ericaceae* continue to be prevalent (Figures 3 and 5).

Pollen zone PiaIV (5 samples; 145.70–138.75 mbsf; 2.74–2.70 Ma): The pollen and spores concentration remains low in this zone (1,106 grains per cubic centimeters on average). After a long downward trend, the abundance of tree/shrub pollen increases again, which is mainly due to an increase of the upper montane forest taxa *Hedyosmum* and Podocarpaceae. Herbs and grass pollen decrease accordingly. *Hedyosmum* pollen has its highest relative abundance in this zone (17%). All Asteraceae pollen (*Artemisia, Ambrosia/Xanthium*, and *Tubuliflorae*) have high relative abundances in this zone.

### 4. Discussion

#### 4.1. On Opening up of the Canopy, Erosion, and Pioneer Taxa

Between ~3.3 and 3.05 Ma, the pollen and spores concentration doubles compared to the preceding and subsequent interval (Figure 4). The two possible mechanisms for this increase are a change of the amount of transported pollen (e.g., through changing climatic conditions resulting in a shift of the pollen source
Figure 4. Palynomorph percentages of ODP Hole 1239A for Amaranthaceae and the four vegetation belts (lowland rainforest = LR, lower montane forest = LMF, upper montane forest = UMF, páramo) from 3.8 to 2.7 Ma. Colored shading represents the 95% confidence intervals (after Maher, 1972). Glacial and interglacial marine isotope stages (MIS) are shown in blue and red, respectively. At the top the U37° sea surface temperatures (SST) of ODP Site 846 (Lawrence et al., 2006) are shown. At the bottom the LR04 global stack of benthic δ18O reflecting changes in global ice volume and deep ocean temperature (Lisiecki & Raymo, 2005), and stable oxygen isotopes of the benthic foraminifer C. wuellerstorfi (Tiedemann et al., 2007) of ODP Hole 1239A are presented. Ages are from Tiedemann et al. (2007). Note the gaps between 3.0 and 2.8 Ma in the record of Site 1239 and the unsure stratigraphic position of MIS G10.
area), or a change of the amount of produced pollen (higher production could be caused by changes in the vegetation cover, especially by an expansion of anemophilous taxa). To disentangle the two mechanisms, we compared the pollen concentrations of selected taxa to their relative abundances (Figure 6) to establish how far relative and absolute abundance run parallel. The pollen concentration reflects the total number of grains deposited per unit volume of sediment and may be used to detect changes in the number of pollen grains reaching the deposition site. These changes may be the result of variations in sedimentation or floristic changes. While pollen percentages are interrelated, concentrations displaying absolute values might reveal changes in the vegetation which would not be detected by looking at the percentages alone. For instance, the relative abundances of Asteraceae Tubuliflorae, Podocarpaceae, Hedyosmum pollen, and Cyatheaceae spores did not increase when their pollen concentration increased between 3.3 and 3.0 Ma. This points towards a general shift of the amount of transported pollen grains. On the other hand, the pollen records of Poaceae, Cyperaceae, Amaranthaceae, Polypodiaceae, Selaginella, and Polylepis/Acaena show an increase in concentration simultaneously with an increase in relative abundance (Figure 6). This pattern probably indicates an increase of the amount of produced pollen/spores due to an expansion of the range of source plants that are larger pollen producers. Most of those taxa are common in open habitats (Polylepis/Acaena, Poaceae, and Cyperaceae in the páramo, Amaranthaceae in coastal deserts and shrubland) which are generally more prone to erosion and provide a greater contact surface for wind. This might be an additional reason for higher pollen concentrations of these taxa. Increased sedimentation rates at ODP Site 1239 between 3.3 and 3.0 Ma of 14 to 17 cm/ka (compared to 10 to 13 cm/ka before and after that; Tiedemann et al., 2007) together with the increased pollen concentration support the argument of a change in the amount of transported pollen; hence, we infer a general shift of the pollen transport around 3.3 Ma accompanied by a shift in the vegetation favoring taxa which produce large amounts of pollen.

What could have caused the shift in pollen transport? Increased precipitation as the direct effect of high SST is unlikely because high pollen concentration does not line up with high SSTs (Figure 4). On a global scale erosion rates increased since 3–4 Ma due to elevated climate instability, in which periods of mass wasting alternated with periods of enhanced transport (Herman & Champagnac, 2016; Peizhen et al., 2001). Regionally, tectonic movements related to a late step of northern Andean uplift might have reshaped the drainage basin to include regions with higher precipitation. Gregory-Wodzicki (2000) suggests that the Colombian Andes were only at 40% of their modern elevation by 4 Ma and reached modern values around 2.7 Ma. Mora et al. (2008) state that the eastern Cordillera of Colombia reached a critical elevation as an orographic barrier between ~6 and 3 Ma. Following mountain uplift, precipitation in the mountain regions would generally have been higher at the luv side of the mountains (and lower downwind—in the shade of the mountains). These regions would have been increasingly susceptible to erosion and higher runoff would have enhanced pollen transport. As this would be a permanent change of the topography and drainage basin, the question remains why the pollen concentration decreased again after ca. 3.1 Ma.

Pioneer plants like Elaphoglossum, Poaceae, Asteraceae (mainly Tubuliflorae, Artemisia), and Ericaceae (Lozano et al., 2007) start expanding from ca. 3.4 Ma on (Figure 5). After the period of increased erosion and pollen transport, they expand further from ~3.1 Ma on. These pioneers presumably colonized the newly created open habitats. After 2.75 Ma, the montane forest trees Hedyosmum and Podocarpaceae recapture the open patches formerly occupied by herbs and grasses.

Our findings overall agree well with the pollen record Funza II from the high plain of Bogotá (Hooghiemstra & Ran, 1994), which is one of the few records of vegetation and climate change in the northern Andes covering parts of the late Pliocene. It overlaps with our record over the time interval from 3.2 to 2.7 Ma. The upper montane forest in Funza II was more open compared to those in the Middle and Upper Pleistocene. Although our record does not extend to the Pleistocene, we also observe a decrease of tree/
shrub pollen and an increase of herbs and grass pollen as well as broad-range taxa in the time interval from 3.6 to 2.7 Ma, indicating more open conditions. Funza II further shows that azonal forests were irregularly formed by pioneers like *Dodonaea* and other taxa like *Ilex*. This would be in agreement with our observation of an increased abundance of *Ilex* (Figure 3).

### 4.2. Developments in the páramo and the Upper Forest Line

Between 3.91 and 3.42 Ma, a regionally warm climate is expressed in our record. High temperatures during this interval are reflected in an upward expansion of the upper montane forest, indicated by an increased abundance of herbs and grass pollen as well as broad-range taxa in the time interval from 3.6 to 2.7 Ma, indicating more open conditions. Funza II further shows that azonal forests were irregularly formed by pioneers like *Dodonaea* and other taxa like *Ilex*. This would be in agreement with our observation of an increased abundance of *Ilex* (Figure 3).
abundance of upper montane forest pollen (e.g., Podocarpaceae) and a decline of páramo pollen. The study area is predominantly covered by closed forests with only few patches of open vegetation beyond the páramo. This is expressed by the highest abundance of tree and shrub pollen of the analyzed period, as well as a low representation of broad-range taxa, a group consisting predominantly of herbs. While the páramo at our study site was floristically very stable in the early Pliocene (4.7–4.2 Ma; Grimmer et al., 2018), new taxa (Sisyrinchium, Orthrosanthus, Puya) appear from 3.75 Ma onwards (Figure 7). This development probably reflects the dynamic nature of this relatively newly established ecosystem and has also been described by Van der Hammen et al. (1973) for the central part of the Colombian Eastern Cordillera. The early Pliocene composition of the páramo (4.7–4.2 Ma) has a clear neotropical signature with Jamesonia/Eriosorus, Huperzia, and Polyplepis/Acaena having immigrated to the páramo from lower elevation habitats of the neotropics and subsequently adapted to new environmental conditions (Sklenár et al., 2011). In contrast, the taxa which appear in the record after 3.75 Ma predominantly immigrated to the area from other floristic realms: Sisyrinchium originally occurred in temperate and cool regions of both hemispheres, and Orthrosanthus had a south temperate distribution (Sklenár et al., 2011). This suggests that the high-elevation ecosystem was first colonized by taxa from proximate habitats of the neotropics, and thereafter, with the progressive formation of the Isthmus of Panama, taxa from more distant locations gradually arrived.

Around 3.5 Ma, a transition occurred from warm climatic conditions with a relatively high upper forest line (high abundance of upper montane forest [UMF]) to colder climatic conditions with a lower forest line (decreased abundance of UMF and increased abundance of páramo vegetation). At the same time, the SST at ODP Site 846 decreased (cf. Figure 4). Additional to the true páramo taxa, the abundance of some broad-range taxa which are assumed to have their main occurrence in the páramo (Tubuliflorae, Poaceae, and Ericaceae) also increased. This is another indication of colder climatic conditions with a lowered forest line. This trend continues through pollen zones PiaII and PiaIII. Páramo pollen has maximum abundances during MG4, M2, and KM2 (Figure 4). This local cooling trend thus starts well before the M2 glacial, which is the first large excursion of the LR04 stack (~3.3 Ma; Lisiecki & Raymo, 2005).

Two taxa which grow predominantly at the upper forest line are Polyplepis/Acaena and Morella (formerly Myrica; M. Kessler, 2002; Marchant et al., 2002). The oscillations of Polyplepis/Acaena are generally opposite to those of the upper montane forest. During warm phases, when the upper montane forest extends to higher altitudes, the abundance of Polyplepis/Acaena is low and vice versa. Morella already appears sporadically in the earliest Pliocene samples and has frequent occurrences from 3.6 Ma onward (Figure 3). This record probably reflects the establishment of Morella in the area. Andriessen et al. (1993) dated the immigration of Morella to the high plain of Bogotá at 3.7–2.7 Ma. Van der Hammen and Hooghiemstra (1997) mention Morella's first appearance before 4 Ma, which is in agreement with our record. The Funza II record
(Hooghiemstra & Ran, 1994) shows that the transitional zone between the upper montane forest and the páramo was abundantly covered with Morella. It is not known whether Morella immigrated to South America only after the establishment of the Panamanian land bridge (Gentry, 1982) or if South America was colonized earlier by long-distance dispersal independent of tectonic processes. Taking into account recent advances in dating the closure of the Central American Seaway (e.g., O’Dea et al., 2016) and results of molecular studies showing that the South American species of Morella went through rapid diversification around 4 Ma (Herbert, 2005), it seems more likely that Morella reached the northern Andes via long-distance dispersal before 4 Ma and established rapidly on the high-altitude open grounds created by Andean uplift.

4.3. Glacial-Interglacial Variability and Comparison With mPWP Modeling

Comparing the pollen record to MIS can yield information about the response of the vegetation to glacial-interglacial climatic variability. When looking at the changing extent of the vegetation belts during glacial and interglacials, it becomes apparent that páramo pollen has maxima during most glacial while lowland rainforest pollen shows glacial minima (Figure 4). Obviously, the expansion and contraction of vegeta-
tion belts with the glacial/interglacial climatic oscillations affects all vegetation belts down to the lowland
rainforest and is not limited to the páramo and upper montane forest. A similar glacial/interglacial vegetation response was found in a late Quaternary pollen record from the Panama Basin (González et al., 2006).

Another observation is that minima in pollen concentration occur during interglacial MIS, while there is no such clear relation between glacial MIS and pollen concentration (Figure 4). The dry indicators, on the other hand, show maxima during some glacials (G6, G10, G22, and MG4). This is interesting because the pollen record does not indicate a clear pattern of dry glacials versus humid interglacials as shown in a multiproxy record of terrigenous input of the late Pleistocene by Rincón-Martínez et al. (2010). Thus, this pattern of cold/dry and warm/wet oscillations seems to have been weaker or not existing in the late Pliocene and must have developed later. The dynamics of the late Quaternary equatorial front-ITCZ system with its large meridional SST gradient during glacials presumably operated differently in the late Pliocene.

Regarding data-model comparison, mainly mid-Piacenzian interglacials have been modeled (Prescott et al., 2014, 2018), but some general conclusions can be drawn for the mPWP. Compared to modern conditions, temperatures are higher in the western Andes and lower in the eastern part of the Andes in the model of Contoux et al. (2012) which is due to changes in topography. Although the Pliocene Andean forest is not analogous to the modern assemblage due to immigration of Northern Hemisphere taxa, our record shows that the relative abundance of upper montane forest pollen was twice as high in the mPWP compared to the Holocene (Figure 8). This would be in agreement with higher temperatures in the western Andes and an elevated upper forest line.

In the models, precipitation over the tropical Pacific Ocean is lower compared to modern which is explained by a slowing down of the Walker circulation due to a reduced zonal SST gradient which induces a broadening of the ITCZ (Chandan & Peltier, 2017; Contoux et al., 2012). Prescott et al. (2014) also mention a possible ITCZ shift related to the altered pole to equator temperature gradient. These findings agree with our inter-
pretation of a drier climate in coastal Ecuador during the mPWP.

Two recent modeling studies (Prescott et al., 2014, 2018) investigated climate variability in and around four different interglacials of the mPWP (MIS G17, K1, KM3, and KM5c) as well as vegetation response to orbital forcing. Comparing model outputs to the palynological record can identify areas of data-model mismatch and validate model performance. Although the resolution of the pollen record does not permit exact compar-
ison with model outputs and uncertainties in the chronology must be taken into account, we can neverthe-
less give a tentative idea of similarities and differences between climate models and our pollen record. The models generally show that in our study area, the simulated changes regarding climate parameters (tempera-
ture and precipitation) and vegetation due to orbital forcing are small (in contrast to, e.g., central and eastern Asia). Concerning the mean annual surface air temperature (SAT), interglacial K1 has slightly higher variability in our study area compared to KM5c. For the seasonal SAT change, the variability during K1 is even larger (Prescott et al., 2014). Surface temperature variability would be reflected in our record mainly through changes in the relative abundances of páramo and upper montane forest pollen, indicating vertical movements of the upper forest line. When comparing the representation of páramo and UMF around the two interglacials (two samples before and two samples after the peak in K1 and KM5c), we
find that the variability in both interglacials is similar. Simulations conducted for KM5c between 3,189 and 3,197 ka all demonstrate a significant terrestrial warming over South America of up to 1°C (Prescott et al., 2014). This is in agreement with the pollen record exhibiting relatively low abundance of páramo pollen compared to a high abundance of UMF pollen. When comparing the modeled development of predicted plant functional types, they remain constant over all four interglacials with around 85%–95% broadleaf forest and 5%–15% grass (Prescott et al., 2018). This shows that the trend of opening up that we see in the pollen record is not reflected in the model predictions. A reason for mismatch might be that smaller changes within the range of 10% are not shown in the model. Furthermore, plant functional types cannot be directly compared to pollen abundances because of differences in pollen production rates across plant types (Prescott et al., 2018).

The models run with prescribed or dynamic vegetation both show higher annual SATs during all interglacials compared to control run KM5c (Prescott et al., 2018). These lower mean annual temperatures during KM5c relative to the other modeled interglacials are not in agreement with our observations of a high abundance of upper montane forest and a low abundance of páramo pollen (high upper forest line) during KM5c (Figure 4). A data-model mismatch could indicate that orbital forcing at this time was not the dominant contribution to climate change, but other factors influencing the vegetation were more important. This could be local or regional (sub-gridscale) features not captured by the model due to the coarse model resolution, or variations in pCO₂ or feedbacks such as aerosol cycles which were not included in the model (Prescott et al., 2018). Interestingly, the model HadCM3 with dynamic vegetation predicts higher
precipitation over Colombia and lower precipitation over coastal Ecuador and the EEP compared to control run KM5c for interglacial G17 (Prescott et al., 2018). At the same time, our pollen record shows an increase of Amaranthaceae pollen from coastal Ecuador while the montane forest is still well represented, and the pollen concentration is moderately high. This could be related to a northward shift/broadening of the ITCZ, as described in the following section.

4.4. Trends in Vegetation and Climate

One of the most obvious trends in this record is the increase of pollen of Amaranthaceae, starting around 3.1 Ma and suggesting an expansion of the coastal desert area. Dry vegetation might have replaced parts of the lowland rainforest which diminished slightly during this period (Figure 8). There is generally less pollen of trees and shrubs and more of herbs and grasses, but humidity in the mountains is still available as shown by the representation of several montane tree and tree-fern taxa, which are humidity dependent (e.g., Hedysosmum, Morella, and Cyatheaaceae). Additionally, the representation of the lower and upper montane forest is rather stable. This suggests that the mountains still received enough rainfall, while the desert area of southern Ecuador expanded. Such a precipitation pattern is typical for La Niña conditions (Vuille et al., 2000). However, the zonal SST gradient in the equatorial Pacific between 3.1 and 2.7 Ma is rather small (Lawrence et al., 2006; Wara et al., 2005; cf. Figure 1), which would not support La Niña conditions and a strong Walker circulation accordingly. This seeming contradiction might be explained by model simulations for the mid-Pliocene warm period that find a precipitation decrease over the tropical Pacific explained by a broadening of the ITCZ due to a weakened Walker circulation and a smaller zonal SST gradient (Contoux et al., 2012). This pattern would be in agreement with the observed hydrological changes in the study area and the reconstructed zonal SST gradient. The model of Chandan and Peltier (2017) shows higher precipitation over the Ecuadorean Andes and an area of lower precipitation over the coastal Pacific for the mPWP compared to modern, which is also in accordance with our record.

The environmental changes in Ecuador after 3.3 Ma took place at around the same time as the first major pulse of ice-rafted debris during M2 (Flesche Kleiven et al., 2002) and might be a precursor of global climate changes leading to the intensification of the Northern Hemisphere glaciation at the start of the Pleistocene. In that case, it would the parallel temperature decline in the Northern Hemisphere as recorded for northern Norway (Panitz et al., 2016), in Lake Baikal in Central Asia (Demske et al., 2002), and Lake El'gygytgyn in northern Siberia (Andreev et al., 2014; Brigham-Grette et al., 2013). Drying coastal climate in Ecuador after 3.1 Ma would have preceded global changes associated with the increase of the Northern Hemisphere glaciation such as strengthening of the NE trade winds at ~2.7 Ma as recorded offshore of West Africa (Vallé et al., 2014), in Chinese Loess sediments (Yang & Ding, 2010), and in North America (Naafs et al., 2012), as well as aridification of Central Asia after 2.6 Ma (Cai et al., 2012; Wu et al., 2007).

5. Conclusions/Outlook

This study aimed to (1) investigate vegetation change in western equatorial South America during the Piacenzian, (2) infer climatic changes from the response of the vegetation, and (3) assess if and how the onset of global cooling is manifested in the study area.

The climate in western equatorial South America was stable and warm from ~3.9 to 3.3 Ma, when a lowered forest line showed first evidence of cooling. After 3.75 Ma, floristic changes occurred in the páramo due to immigration of taxa from distant locations. A doubling of the pollen and spores concentration occurred between ~3.3 and 3.05 Ma, caused by a general shift of the pollen transport accompanied by a shift in the vegetation favoring taxa which produce large numbers of pollen. The increased pollen transport may have been an effect of increased erosion rates due to tectonic processes and/or climate change (e.g., increased precipitation). After 3.1 Ma, the open habitats created by erosion were colonized by pioneer plants.

Shifts of the upper forest line after 3.5 Ma indicate temperature fluctuations towards cooler conditions. After 3.1 Ma, an increase of Amaranthaceae pollen suggests an expansion of the coastal desert area while the montane forests still received abundant rainfall. This pattern is most likely caused by a precipitation decrease over the coastal areas which can be explained by a broadening of the ITCZ due to a weakened Walker circulation. This explanation is in agreement with SST reconstructions (Etourneau et al., 2010; Lawrence et al., 2006; Wara et al., 2005) and modeling results for the mid-Pliocene warm period (Contoux et al., 2012).
The isochronous occurrence of environmental changes in the present record with the first major pulse of ice-rafted debris as well as cooling temperatures in the Northern Hemisphere suggests that these changes might be a precursor of the intensification of the Northern Hemisphere glaciation.

We hope that this study will be a valuable contribution to improving global land surface reconstructions. Future work should focus on an extension of the record into the Pleistocene, which could give more insights into the timing of the strengthening of the Walker circulation. Further modeling studies could shed light on the role of the tropics in the onset of NHG.

**Conflict of Interest**

The authors have no competing interests to declare.

**Data Availability Statement**

The underlying research data are stored in PANGAEA as data set (https://doi.org/10.1594/PANGAEA.921208).

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