

First, we would like to thank the referees and reviewers for their insightful and helpful comments. Below please find a point by point reply to all comments, with our replies marked as “RESPONSE”. The changes made in the original manuscript are highlighted in yellow. A marked-up manuscript version is attached.

Interactive comment on “Early Pliocene vegetation and hydrology changes in western equatorial South America” by Friederike Grimmer et al.

PAGES Data Review Team

darrell.kaufman1@gmail.com

Received and published: 18 November 2017

The PAGES Data Stewardship Integrative Activity seeks to advance best practices for sharing the data generated and assembled as part of all PAGES-related activities. The CP Special Issue, “PAGES Young Scientists Meeting 2017” is part of this PAGES activity. The co-editors of the Special Issue are reviewing the data availability within each of the CP-Discussion papers in relation to the CP data policy (https://www.climate-of-the-past.net/about/data_policy.html) and current best practices. The editor team is making recommendations for each paper, with the goal of achieving a high and consistent level of data stewardship across the Special Issue. We recognize that an additional effort will likely be required to meet the high level of data stewardship envisaged, and we appreciate the dedication and contribution of the authors. This includes the use of

C1

Data Citations (see example below). Authors are also strongly encouraged to deposit significant code into a suitable repository and to cite it using a Data Citation.

We ask authors to respond to our comments as part of the regular open interactive discussion. If you have any questions about PAGES Data Stewardship principles, please contact any of us directly. Best wishes for the success of your paper.

YSM Special Issue editor team

Y. Zhang, D.S. Kaufman, H. Plumpton, R. Barnett, M.F. Loutre, M.N. Evans, S.C. Fritz, C. Tabor, E. Razanatsoa, and E. Dearing Crampton Flood

For this paper:

(1) Research input data – proxy and instrumental datasets

This research contribution includes published proxy data in Figures 6-7, including, (i) $\delta^{18}\text{O}$ record of *G. tumida*/*G. sacculifer* at ODP site 851 from Cannariato and Ravelo (1997), (ii) Mg/Ca and $\delta^{18}\text{O}$ record of *G. tumida* at ODP Site 1239 from Steph et al. (2005, 2010), (iii) alkenone-based SST record of core ODP 846 (Lawrence et al., 2006), which are already available through existing data repositories. In order to adhere to the Data Policy for Climate of the Past, URLs or full data citations to the primary data must be included in the Data Availability section.

The source of the datasets used to generate Figure 2 are incomplete in the figure caption. Figure 2a: As stated on the NOAA-ESRL website, a bibliographic citation must be included to reference the publication that describes the specific reanalysis product used for the SST field. This is in addition to acknowledging the ESRL for the use of the online data-analysis tool. Figure 2b: Please provide a complete citation for the source of the terrestrial biome map.

(2) Research output data – pollen

This paper presents new and valuable pollen assemblage data from equatorial South

C2

America. In order to adhere to the Data Policy for Climate of the Past, these new data together with (i) the 95% confidence intervals and (ii) the corresponding chronological ages (as showed in Figures 4-5) must be uploaded to an established online data repository (e.g., Neotoma), and a Data Citation or URL link for access to these data must be provided in the Data Availability section of the paper.

What is a “Data Citation”?

Data Citations track the provenance of a dataset giving credit to the data generator; this is in addition to any references to publications where the data are described. Data Citations are used in the text (or tables) alongside and in the same way as publication citations. In the Reference list, they include: Creators, Title, Repository, Identifier, Submission Year. More information about Data Citations is here: <<https://www.datacite.org/mission.html>> Here is an example of text and corresponding citations (using CP punctuation style):

“The PAGES2k Consortium (2017a) assembled a large global dataset of temperature-sensitive proxy records (PAGES2k Consortium, 2017b). Among the records is the paleo-temperature reconstruction from Laguna Chepical (de Jong et al., 2016), which was described by de Jong et al. (2013).”

References

de Jong, R., von Gunten, I., Maldonado, A., and Grosjean, M.: Late Holocene summer temperatures in the central Andes reconstructed from the sediments of high-elevation Laguna Chepical, Chile (32° S), *Climate of the Past*, 9, 1921-1932, 2013.

de Jong, R., von Gunten, I., Maldonado, A., and Grosjean, M.: Laguna Chepical summer temperature reconstruction, World Data Center for Paleoclimatology, <https://www.ncdc.noaa.gov/paleo/study/20366>, 2016.

PAGES 2k Consortium: A global multiproxy database for temperature reconstructions of the Common Era, *Scientific Data*, 4,170088, 2017a.

C3

PAGES 2k Consortium: A global multiproxy database for temperature reconstructions of the Common Era, version 2.0.0, figshare, <https://figshare.com/s/d327a0367bb908a4c4f2>, 2017b.

Interactive comment on *Clim. Past Discuss.*, <https://doi.org/10.5194/cp-2017-129>, 2017.

C4

Interactive comment on “Early Pliocene vegetation and hydrology changes in western equatorial South America” by Friederike Grimmer et al.

Friederike Grimmer et al.

fgrimmer@marum.de

Received and published: 26 June 2018

Data are uploaded in Pangaea as datasets PANGAEA.884280 and PANGAEA.884153, which are combined in PANGAEA.884285. We update and complete these datasets (upload in progress) with the data from the new supplementary figure.

Interactive comment on Clim. Past Discuss., <https://doi.org/10.5194/cp-2017-129>, 2017.

Interactive comment on “Early Pliocene vegetation and hydrology changes in western equatorial South America” by Friederike Grimmer et al.

S. Flantua

s.g.a.flantua@gmail.com

Received and published: 26 November 2017

Review Report by Henry Hooghiemstra and Suzette Flantua

Clim. Past Discuss., <https://doi.org/10.5194/cp-2017-129>

Grimmer, F., Dupont, L., Lamy, F., Jung, G., González, C., Wefer, G., Early Pliocene vegetation and hydrology changes in western equatorial South America.

Background comments on North Andean uplift and terrestrial fossil pollen records: The present paper focusses on the complex history of Andean orogenesis in northwestern South America as seen from marine sediments. An approach from the marine sediment archive is a welcome addition to terrestrial evidence. The lack of well dated sediments in the terrestrial basins fueled much speculation about the uplift history of

C1

the northern Andes, which is strongly related to the closure of the Panamanian Isthmus. Van der Hammen & González (1964) were among the first to speculate how vegetation change could be interpreted in terms of an Andean uplift history.

This discussion was fueled with more data by Van der Hammen et al. (1973). More detailed paleobotanical and palynological evidence was elaborated by Wijninga (1996). A synthesis was published by Hooghiemstra et al. (2006). Indeed, at that time significant uplift of the Colombian Andes was thought to be of Pliocene age a.o. supported by the species-poor páramo (called ‘protopáramo’) at the base of the Funza-1 pollen record (Hooghiemstra, 1984). The Funza-2 record from the Bogotá basin extended the Funza-1 record back in time, but the age model of the Bogotá sediments continued to be uncertain (Andriessen et al., 1993). A break through in developing an adequate age model was developed by Lucas Lourens (Torres et al. 2013) and the complete Bogotá sediments appeared to reflect the last 2.25 Ma, thus significantly younger as previously thought. In the meantime, mountain building chronology based on apatite fission-track data (Hoorn et al., 2010; see Supplementary Information Fig. S1) showed ages of 30-15 Ma for the most of the Ecuadorian Andes, and ages of 25-10 Ma for most of the Colombian Andes, whereas uplift in specific parts of the Colombian Andes, the Cocuy area in particular, was dated 10-5 Ma.

One may expect that páramo vegetation developed, once a significant proportion of the Andes reached over the elevation of the upper forest line (UFL). Thus, an age of around 10 Ma for the development of the páramo biome is feasible, but so far has been without evidence. In Torres et al. (2013), the species-poor ‘proto-paramo’ is dated c. 2 Ma. Indeed, molecular phylogenies of high Andean taxa show much and rapid speciation during the Quaternary, mainly driven by the Quaternary ice ages (Van der Hammen, 1974; Diazgranados and Barber, 2017; Pouchon et al., accepted; Flantua and Hooghiemstra, 2017 in Flantua PhD thesis and in book chapter 2018). With the present-day understanding, a much longer history of the development of páramo biome during late Miocene and Pliocene times seems feasible. In absence of strong

C2

climate cycles during pre-Quaternary times (Flantua and Hooghiemstra, in PhD thesis 2017, in book chapter 2018), it may be expected that diversification of the páramo flora increased at low levels during late Miocene and Pliocene times (mainly by migration?; see Baumann, 1988), and speciation shows an explosive increase during the last 2 Ma (see the increasing numbers of studies on molecular phylogenetic trees).

In the absence of long terrestrial records of páramo evolution, pollen analysis of marine sediment cores may provide us with the lacking information. Therefore, the present paper has a fascinating potential to shed new light on this long debated issue. However, I am not surprised that a marine sediment record at this location is only registering weakly the vegetation changes from the adjacent continent. Comparing the regional setting of pollen source areas and operating transport mechanisms in the Eastern Pacific off Ecuador with e.g. the NW African setting (Hooghiemstra et al., 2006), expectations for successful research are relatively poor for the northern Andes. In this respect, the 2006-paper has some predicting power for research in other parts of the world. Notwithstanding potential limitations, the present study is a logical step in exploring the potential of using marine sedimentary archive for insights into continental processes.

Specific comments in text:

line 15: The pollen record presented in this paper reflects the interval 4.7-4.2 Ma only in 46 pollen samples. There is no justification why not a longer interval has been analysed.

18: The sediment core is located at the equator and one may wonder which area is considered as 'study area'. Fig. 2b offers the possibility to better show the potential pollen transport routes from the various source areas to site ODP 1239. We guess that pollen source areas stretch more to the south than to the north.

30: Montes 2015 should be Montes et al. 2015. If you really want to capture the discussion around the closure, then you should already add here: O'Dea A, Aguilera O, Aubry M-P, Berggren WA, Budd AF, Cione AL, Coates AG, Collins LS, Coppard SE,

C3

Cozzuol MA, de Queiroz A, Duque-Caro H, Eytan RI, Farris DW, Finnegan S, Gasparini GM, Grossman EL, Johnson KG, Keigwin LD, Knowlton N, Leigh EG, Leonard-Pingel JS, Lessios HA, Marko PB, Norris RD, Rachello-Dolmen PG, Restrepo-Moreno SA, Soibelzon E, Soibelzon L, Stallard RF, Todd JA, Vermeij GJ, Woodburne MO, Jackson JBC. 2016a. Formation of the Isthmus of Panama. *Science Advances*. e1600883. A. O'Dea, H. A. Lessios, A. G. Coates, R. I. Eytan, S. A. Restrepo-Moreno, A. L. Cione, L. S. Collins, A. de Queiroz, D. W. Farris, R. D. Norris, R. F. Stallard, M. O. Woodburne, O. Aguilera, M.-P. Aubry, W. A. Berggren, A. F. Budd, M. A. Cozzuol, S. E. Coppard, H. Duque-Caro, S. Finnegan, G. M. Gasparini, E. L. Grossman, K. G. Johnson, L. D. Keigwin, N. Knowlton, E. G. Leigh, J. S. Leonard-Pingel, P. B. Marko, N. D. Pyenson, P. G. Rachello-Dolmen, E. Soibelzon, L. Soibelzon, J. A. Todd, G. J. Vermeij, J. B. C. Jackson. Building bridges. Response to Erkens and Hoorn: "The Panama Isthmus, 'old', 'young' or both?". *Science Advances* 2016b: Vol. 2, no. 8, e1600883 DOI: 10.1126/sciadv.1600883

33. See also figure 1 from O'Dea et al. 2016b

57: 'Northern Andes' needs to be better specified as the uplift history in Ecuador differs from Colombia.

63: Additionally to Spikings et al. 2005: see Supplementary Information Fig. S1 in Hoorn et al., 2010.

74: first palynological record = first marine palynological record. Pollen records of Pliocene age are Rio Frio-17 and Subachoque-39 (Wijninga, 1996 figures 8.2 and 8.4; Hooghiemstra et al., 2006 figures 4 and 7) that show the floral composition of montane forest and páramo. Table 4 of the 2006-paper may be helpful in considering how pollen taxa are grouped to reflect the altitudinal vegetation zones.

81: make a difference between the 'Western Cordillera' in Ecuador and the 'Western Cordillera' in Colombia (see also lines 62-63).

C4

85: Figure 2b shows 'terrestrial biomes' in 7 legend units. However, this palynological study is using 4 legend units (the left hand four in Table 1). The link between pollen source areas and pollen diagram can be improved if for consistency Figure 2b would show the same categories as recognized in Table 1. Fig. 2b can be improved by indicating with arrows the routes and mechanisms (ocean currents, rivers, wind?) of pollen and spore transport towards ODP 1239. The information of the inset figure can be placed (with less detail) in the main figure.

95: The acronym ENSO has been introduced already in line 49.

96: Marchant et al., (2001) is a good example of small-scale climate patterns.

118: Here you specify "the mountains" as the area within Ecuador, while before you talk broadly about the "Northern Andes". For consistency, the Ecuadorean Andes/Cordilleras should be used throughout the paper.

127: Palmae = Arecaceae

141: Santiago river not shown in map?

140-141 & 162: The combination of pollen and fern spores in the pollen sum is not ideal. In Lowland Forest (< 1000 m) and Lower Montane Forest fern-loaded trees fallen across small rivers shed enormous amounts of spores directly into the water currents (personal observations). Therefore, the proportion of fern spores in the pollen spectra are of a different character than the proportion of pollen, and both components are difficult to compare (see also figures 72-75 in Hooghiemstra et al., 1986).

143: It would be very useful to have figure 2 show these geographical features such as the Carnegie Ridge and Peru-Chile Trench, and show how pollen would reach the location of the record. 153-154: What is the potential pollen supply by the Humboldt Current? and where could pollen source areas be located? Furthermore, from this description it's not clear why you are expecting to find signals from the eastern lowlands which constitute the western margin of the Amazon Basin (line 118).

C5

156: Avoid starting the sentence with a number. See 191.

183 / Table 1: (a) Table 1 shows an effort to group pollen and spore taxa into meaningful ecological groups. A marine pollen record has a wide pollen source area and many taxa listed do have a wide ecological range. The latter makes it difficult to develop clear-cut ecological groups. Páramo: Several 'páramo' taxa also occur in the forest; Upper Montane Forest: Melastomataceae from the UMF also occur abundantly in the páramo; Lowland Forest (LF): is represented by a remarkably low number of taxa; Broad-range taxa: Poaceae indeed have a broad ecological range, but most of it comes from páramo and also dry vegetation in coastal areas and interandean valleys; Asteraceae Tubuliflorae also have a wide range but the bulk is from the páramo; Artemisia seems from Peruvian origin?; Thevetia is indicator of dry conditions rather than a broad range plant; Humid indicators: the following 4 taxa are advised to be omitted from this list: Ranunculaceae (important plant in the puna), Ilex (indeed, also in wet forest but frequently elsewhere), Myrica (= Morella), and Malpighiaceae (also in savannas).

(b) A significant proportion of Lowland Forest (including wet rainforest and dry deciduous forest) and Lower Montane Forest is palynologically 'silent' as many trees are pollinated by insects, beetles, etc. Given the northward flow of the Humboldt Current, and atmospheric circulation in the direction of the coast, I am not surprised that LF is hardly represented by taxa in Table 1. Palms are more abundant in Lower Montane forest (LMF); by moving the Arecaceae from the category LF to LMF, LF is hardly reflected at all. This has consequences for the interpretation and conclusions.

(c) Most of the taxa in the category 'páramo' occur in the ecotone zone of the UMF. Thus the record for 'páramo' as based on the taxa listed in Table 1 may also reflect the zone with dwarf forest and shrub. (d) In Flantua et al. (2014, figure 7) we explored how altitudinal vegetation zonation is reflected on the basis of GBIF data. We were quite disappointed with the poor altitudinal zonation, possibly explained by a large amount of 'noise' in the GBIF data by using data from a wide geographical region. We concluded

C6

that up to date an altitudinal zonation based on expert knowledge from field botanists gives better results: see Groot et al., 2013 (RPP) figure 3).

185: Here, make also reference to Van der Hammen (1974).

188: Which taxa occurred in less than 10% ? A Table showing all identified pollen and spore taxa and their assessment to ecological categories would be helpful.

192: to what refers 'respectively'?

194: 26-27% ? Does this relate to a figure?

197: Where is the replacement of Podocarpus by Alnus shown in a figure?

207: 'The Lowland Rainforest is mainly represented by Polypodiaceae'. However, Polypodiaceae actually occur everywhere and are not a representative of lowland rainforest in particular. Figure 4: curves are easier to read with a horizontal line at 0%. The elevation indicated for páramo and UFL overlap by 100 m. Is this on purpose? Can your modern samples be shown here as well for comparison?

217-237: make reference to the figure where all these changes can be seen.

229: 'of the pollen sum' is redundant.

232-233: Podocarpus excluded from the UMF; if I understand well, not from the pollen sum.

240: 2 out of the 3 species mentioned also occur in the forest (Polylepis, Huperzia). The species mentioned are not a strong indication of the presence of páramo. Lycopodium with foveolate spores is most characteristic of páramo vegetation (Van 't Veer et al., 1992); absence of Lycopodium fov. in the pollen spectra is in support of the view that the present taxa identified as 'reflecting páramo' also are reflecting lowermost páramo and ecotone forest.

245: Fig. 5: where is the curve showing páramo vs. montane forest? 'páramo sum' is

C7

a confusing term; better to use 'paramo taxa (%)'

251-253: difficult to understand why the evidence mentioned is suggesting drier conditions. Please explain more clearly.

255: better to show the location of TR 163-38 on the map in Fig. 2.

267: difficult to understand the claim '(below the forest line)'. How can open grassland below and above the UFL be identified and separated from each other? This seems an over-interpretation of the data.

270: 'expansion of savannas' ? whereas (line 266) there is a near absence of open grasslands.

272: 'All altitudinal vegetation belts are already present'. Most possibly correct but not necessarily in its present form. For example, after Quercus had changed the composition of montane forest (LMF and UMF) several LMF taxa were able to reach higher elevations (Hooghiemstra, 1984; Torres et al., 2013). Unfortunately, modern climatological constraints of the lower and upper boundaries of the LMF are insufficiently understood (Hooghiemstra et al., 2012); as a consequence it is difficult to infer climatological change from altitudinal migrations of LMF.

272: 'goes through the most prominent' is unclear, please rephrase.

278: 'It is known from other Andean pollen records' The comparison made here should be better explained.

277: 'show a similar pattern of expansion': what do you mean exactly?, and where can the reader see this expansion?

279-282: unclear text, needs rephrasing. For instance, unclear use of 'opposing', what pattern is exactly to be seen in the fig. 5, what is the "more general pattern"?

287 'the main transport agent for pollen' ; I guess also for spores? Replace here and in the following sentences "El Niño" by ENSO.

C8

292: it would be useful to have a figure that can support this statement on 'lowland rainforest of the coastal plain further north' as it's unclear what "further north" is. Or indicate with lat/long values.

294: 'lowland rainforest' is poorly reflected by the taxa listed in Table 1. and as a consequence it is difficult to make a comparison.

298: Difficult to understand what means 'the development of pollen values is decoupled from'. Needs a better explanation and visualization.

300 'eolian' transport is contra to line 140-141.

317: 'Besides being influenced by hydrological changes and wind strength' is unclear and needs further explanation.

321: Replace western Andean Cordillera with western Cordillera of Ecuador. Be consistent throughout the text with Western or western.

324: Sums of upper montane forest = Representation (%) of upper montane forest

334: better to use the more recent reference '(Hoorn et al., 2010)'

333+335: Add 'Ecuador' to Eastern and Western Andean Cordillera

342: In order to use páramo vegetation = In order to use the abundance of páramo vegetation

343: Replace 'no true páramo endemics' by 'Although no taxa restricted to páramo only were identified. ...'

347: 'Polylepis is reaching 5000 m in the northern Andes': I guess this refers to Peru and Bolivia and maximum elevations relate to individual trees. In Colombia and Ecuador Polylepis dwarf forest occurs up to 4200-4300 m.

349-351: Perhaps not as present in montane forest and lowland rainforest, but relatively close to your marine record, you have the presence of several major forest nuclei of

C9

seasonally dry tropical forest biome (see Särkinen et al. 2011) and there are a number of different species of Asteraceae in Peruvian seasonally dry tropical forest (see book Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation by T. Pennington & J. Ratter 2006). Could this biome be the source of Asteraceae in your record?

354: 'without changes in composition' is rather meaningless as so few páramo taxa have been identified.

355: which evidence is fueling this assumption?

356-357: the weak evidence of páramo does not allow to infer conclusions about the elevation of the Andes.

362-368: uplift histories of the various areas are confusing here: 362: indeed uplift is older as can be seen in Hoorn et al., 2010.

364: uplift of the Central Andes is 60-25 Ma (instead of 10-6 Ma; see Hoorn et al., 2010, Suppl. Info.)

365: Amazon fan = Amazon Fan

365: Which is the first palynological paper to state here "in another recent palynological study..?"

366: The Hoorn et al. 2017 paper suggests but does not provide conclusive evidence that the grass pollen are from páramo as the source area for the Amazon river include also high Andean open vegetation of the puna. This sentence here should be rephrased to not 'oversell' Hoorn et al. 2017 in support of páramo presence.

377: Amaranthaceae and Thevetia rather are reflecting dry conditions.

379: what is the meaning of 'all altitudinal vegetation belts go through simultaneous shifts of expansion and retreat' ?

C10

382: Add space before the 3.

385: Better explain 'parallel expansion and retreat of all vegetation belts'. For the last 20 ka we have learned that little goes parallel (see Hooghiemstra and Van der Hammen, 2004).

419: Eastern Cordillera reached = Eastern Cordillera of Colombia reached

421: 'argue for a rapid rise of the region since 4-6 Ma' ; This is outdated and should be 30-5 Ma (see Hoorn et al., 2010 Suppl. Info.)

425: 'Our pollen record from the páramo shows' This conclusion seems unwarranted as the evidence for páramo vegetation is weak and also could reflect ecotone forest and/or other biomes.

435: On which evidence is this sentence based?

440: Conclusion 2 is difficult to understand: when? a shift to what?

441: Higher representation of Podocarpaceae is interpreted as evidence of more intense trade winds. However, this is not necessarily the case as pollen record Funza09 (Torres et al., 2013, figure 10) shows that Podocarpus is more abundant during several intervals of Pleistocene time, potentially also leading to high representation in the marine sediments.

447-448: The presence of páramo is weakly supported by evidence; the inferred altitude of the Ecuadorian (?) Andes is speculative as a consequence.

449-450: Better to refer to more recent literature in which the uplift of the Northern Andes has been set back in time already.

564: Reference Montes et al. 2015 is incomplete.

Fig. S1: To which degree modern core top samples are comparable to the pre-Quaternary samples? Are mechanisms of pollen transport comparable? Some re-

C11

marks about this issue are missing.

Fig. S2: % sum páramo = páramo (place the word 'percentage' in the figure caption) : also for other taxa

Fig. S3: Mention in the caption 'Pollen percentage diagram' and omit all % % indications on top of the pollen diagram. And: Myrica = Morella

IN CONCLUSION:

* The biomes 'páramo' and 'lowland rainforest' are hardly reflected by characteristic pollen and spore taxa. Several taxa now classified as 'broad range taxa' could be shifted to 'páramo' but with the same restriction that these taxa also could reflect uppermost montane forest (ecotone forest).

* In marine pollen records changing proportions of pollen taxa / ecological groups may reflect vegetation change and / or changes in pollen transport. In the present manuscript the latter is hardly/not considered (This remark also relates to the suggestions for improvement of Fig. 2).

* Integration of terrestrial and marine proxies is a powerful tool to maximize conclusions. The comparison with model output has broadened the scope of this paper but – apart from speculation - has not generated an incremental step forwards.

* Pollen zones in Fig. S3 are not expressive and the interpretation in terms of environmental change is not convincing. The presented pollen evidence does not allow a full support of the suggested conclusions of this paper. Analysing a much longer interval has the potential to strengthen conclusions, but the regional setting will remain poor to obtain convincing evidence.

References mentioned in the report:

Andriessen, P.A.M., Helmens, K.F., Hooghiemstra, H., Riezebos, P.A., Van der Hammen, T., 1993. Absolute chronology of the Pliocene-Quaternary sediment sequence of

C12

the Bogotá area, Colombia. *Quaternary Science Reviews* 12, 483-501.

Baumann, F., 1988. Geographische Verbreitung und Ökologie südamerikanischer Hochgebirgspflanzen. Beitrag zur Rekonstruktion der quartären Vegetationsgeschichte der Anden. *Physische Geographie* 28, 206 pp. Geographische Institut der Universität, Zürich.

Diazgranados, M., Barber, J.C., 2017. Geography shapes the phylogeny of frailejones (Espeletiinae Cuatrec., Asteraceae): a remarkable example of recent rapid radiation in sky islands. *PeerJ* 5, e2968. <https://doi.org/10.7717/peerj.2968>

Flantua, S.G.A., Hooghiemstra, H., 2017. Unravelling the mountain fingerprint: topography, paleoclimate and connectivity as drivers of contemporary biodiversity pattern in the Northern Andes. In: Flantua, S.G.A. (ed.), *Climate change and topography as drivers of Latin American biome dynamics*. PhD thesis, University of Amsterdam, pp. 265-307.

Flantua, S.G.A., Hooghiemstra, H., 2018. Historical connectivity and mountain biodiversity. In: Hoorn, C., Parrigo, A., Antonelli, A. (eds.), *Mountains, climate and biodiversity*. Wiley, Chichester, UK.

Groot, M.H.M., Hooghiemstra, H., Berrio, J.-C., Giraldo, C., 2013. North Andean environmental and climatic change at orbital to submillennial time-scales: vegetation, water-levels, and sedimentary regimes from Lake Fúquene during 130-27 ka. *Review of Palaeobotany and Palynology* 197, 186-204.

Hooghiemstra, H., 1984. Vegetational and climatic history of the high plain of Bogota, Colombia: a continuous record of the last 3.5 million years. *Dissertationes Botanicae* 79, 368 pp.

Hooghiemstra, H., Van der Hammen, T., 2004. Quaternary ice-age dynamics in the Colombian Andes: developing an understanding of our legacy. *Philosophical Transactions of the Royal Society London B* 359, 173-181.

C13

Hooghiemstra, H., Agwu, C.O.C., Beug, H.-J., 1986. Pollen and spore distribution in recent marine sediments: a record of NW-African seasonal wind patterns and vegetation belts. *Meteor' Forschungs Ergebnisse, Reihe C* 40, 87-135.

Hooghiemstra, H., Lézine, A.-M., Leroy, S.A.G., Dupont, L., Marret, F., 2006. Late Quaternary palynology in marine sediments: a synthesis of the understanding of pollen distribution patterns in the NW African setting. *Quaternary International* 148, 29-44.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, J., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T., Antonelli, A., 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330, 927-931.

Marchant, R., Behling, H., Berrio, J.C., Cleef, A., Duivenvoorden, J., Hooghiemstra, H., Kuhry, P., Melief, B., Van Geel, B., Van der Hammen, T., Van Reenen, G., Wille, M., 2001. Mid- to late-Holocene pollen-based biome reconstructions for Colombia. *Quaternary Science Reviews* 20, 1289-1308.

Torres, V., Hooghiemstra, H., Lourens, L.J., Tzedakis, P.C. 2013. Astronomical tuning of long pollen records reveals the dynamic history of montane biomes and lake levels in the tropical high Andes during the Quaternary. *Quaternary Science Reviews* 63, 59-72.

Van der Hammen, T. & González, E. (1964). A pollen diagram from the Quaternary of the Sabana de Bogota (Colombia) and its significance for the geology of the northern Andes. *Geologie en Mijnbouw* 43, 113-117.

Van der Hammen, T., Werner, J.H. & Van Dommelen, H., 1973. Palynological record of the upheaval of the Northern Andes; a study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera and the early evolution of its high-Andean biota. *Palaeogeography Palaeoclimatology Palaeoecology* 16, 1-122.

C14

Van 't Veer, R., Ran, E.T.H., Mommersteeg, H.J.P.M., Hooghiemstra, H., 1995. Multivariate analysis of the middle and late Pleistocene Funza pollen record of Colombia. *Mededelingen Rijks Geologische Dienst* 52, 195-212.

Wijninga, V.M., 1996. Paleobotany and palynology of Neogene sediments from the high plain of Bogotá (Colombia): evolution of the Andean flora from a paleoecological perspective. PhD thesis, University of Amsterdam, The Netherlands, 370 pp.

Henry Hooghiemstra, Suzette Flantua

University of Amsterdam

26 November 2017

Interactive comment on *Clim. Past Discuss.*, <https://doi.org/10.5194/cp-2017-129>, 2017.

Interactive comment on “Early Pliocene vegetation and hydrology changes in western equatorial South America” by Friederike Grimmer et al.

Friederike Grimmer et al.

fgrimmer@marum.de

Received and published: 26 June 2018

RESPONSE We thank Flantua and Hooghiemstra for the background information on scientific history.

FLANTUA Specific comments in text:

line 15: The pollen record presented in this paper reflects the interval 4.7-4.2 Ma only in 46 pollen samples. There is no justification why not a longer interval has been analysed.

RESPONSE The period studied in detail covers half a million years, which should be enough to cover the climatic variability. The window was chosen to cover the period of closure of the CAS as indicated by divergence of salinity of the surface waters be-

C1

tween the Caribbean and the Eastern Pacific and highlighted in Fig. 1 (Figure 1 and Introduction lines 35-39).

FLANTUA line 18: The sediment core is located at the equator and one may wonder which area is considered as ‘study area’. Fig. 2b offers the possibility to better show the potential pollen transport routes from the various source areas to site ODP 1239. We guess that pollen source areas stretch more to the south than to the north.

RESPONSE We'll change Figure 2 to better illustrate land-sea connections and the pathways of pollen transport (see separate file AC2). We consider western Ecuador, northernmost Peru and southwestern Colombia the main source areas of pollen and spores in sediments of ODP Site 1239. We'll add to Section 1.1.2: the following two paragraphs replacing lines 139-143):

“Rincon-Martínez et al. (2010) showed that the terrigenous sediment supply at ODP Site 1239 during Pleistocene interglacials is mainly fluvial and input of terrestrial material drop to low amounts during the drier glacial stages. In addition, transport of pollen and spores to the ocean is mainly fluvial (González et al., 2010). High rates of orographic precipitation characterize the western part of equatorial South America. These heavy rains quickly wash out any pollen that might be in the air and result in large discharge by the Ecuadoran Rivers (Fig. 2). Esmeraldas and Santiago Rivers mainly drain the northern coastal plain of Ecuador, and the southern coastal plain is drained by several smaller rivers, which end in the Guayas River. Moreover, the predominantly westerly winds (Fig. 2) are not favorable for eolian pollen dispersal to the ocean. Nevertheless, some transport by SE trade winds is possible and should be taken into account.

“After reaching the ocean pollen and spores might pass the Peru-Chile Trench; which is quite narrow along the Carnegie Ridge, by means of nepheloid layers at subsurface depths. Some northward transport from the Bay of Guayaquil by the Coastal Current (Fig. 2) is likely. However, the Peru-Chile Current flows too far from the coast to

C2

have strong influence on pollen and spore dispersal. We consider western Ecuador, northernmost Peru and southwestern Colombia the main source areas of pollen and spores in sediments of ODP Site 1239.”

FLANTUA I.30: Montes 2015 should be Montes et al. 2015.

RESPONSE We'll correct Montes 2015 into Montes et al. 2015, also in the reference list.

FLANTUA If you really want to capture the discussion around the closure, then you should already add here: O'Dea et al. 2016a. Formation of the Isthmus of Panama. Science Advances. O'Dea et al. 2016b Building bridges. Response to Erkens and Hoorn: “The Panama Isthmus, ‘old’, ‘young’ or both?” Science Advances

RESPONSE O'Dea et al. (2016) has been cited on line 31.

FLANTUA I.33. See also figure 1 from O'Dea et al. 2016b

RESPONSE We prefer our Figure 1 focusing on the surface water exchange between Caribbean and Eastern Pacific over the schematic figure of O'Dea et al. 2016b, because we'll later focus on changes in hydrology. We avoid a discussion about biogeography and faunal exchange between the Americas because this is beyond the scope of the paper.

FLANTUA I.57: ‘Northern Andes’ needs to be better specified as the uplift history in Ecuador differs from Colombia.

RESPONSE The paragraph concerns aspects of the uplift of both the Ecuadorian Andes, the Central Andes, and the Eastern Cordillera of Colombia. We thus describe the uplift of the Ecuadorian Andes in a wider context, while specific remarks about the Andes of Ecuador are given at lines 61, 104 and 363. We'll specify Ecuadorian Andes at lines 357, 425 and 445.

FLANTUA I.63: Additionally to Spikings et al. 2005: see Supplementary Information

C3

Fig. S1 in Hoorn et al., 2010.

RESPONSE Hoorn et al. (2010) reviews Spikings et al. (2005). We prefer the primary reference.

FLANTUA I.74: first palynological record = first marine palynological record. Pollen records of Pliocene age are Rio Frio-17 and Subachoque-39 (Wijninga, 1996 figures 8.2 and 8.4; Hooghiemstra et al., 2006 figures 4 and 7) that show the floral composition of montane forest and páramo.

RESPONSE We'll add a reference to the work of Wijninga and alter the sentence at lines 73-75 to: “While other palynological studies of the region have been conducted for the mid-Pliocene to Holocene (González et al., 2006; Hooghiemstra, 1984; Seillès et al., 2016), only a few palynological records for the early Pliocene exist (Wijninga and Kuhry, 1990; Wijninga, 1996).”

FLANTUA Table 4 of the 2006-paper may be helpful in considering how pollen taxa are grouped to reflect the altitudinal vegetation zones.

RESPONSE We do not understand how Table 4 of Hooghiemstra et al. (2006) could help in the classification of elements like Polylepis/Acaena. No specific pollen types for the páramo vegetation are listed in this table (only the broad range families Poaceae, Ericaceae and Asteraceae).

FLANTUA I.81: make a difference between the ‘Western Cordillera’ in Ecuador and the ‘Western Cordillera’ in Colombia (see also lines 62-63).

RESPONSE We'll change “Western Andean Cordillera of western equatorial South America” into “western Andean Cordillera of Ecuador”

FLANTUA I.85: Figure 2b shows ‘terrestrial biomes’ in 7 legend units. However, this palynological study is using 4 legend units (the left hand four in Table 1). The link between pollen source areas and pollen diagram can be improved if for consistency Figure 2b would show the same categories as recognized in Table 1. Fig. 2b can be

C4

improved by indicating with arrows the routes and mechanisms (ocean currents, rivers, wind?) of pollen and spore transport towards ODP 1239. The information of the inset figure can be placed (with less detail) in the main figure.

RESPONSE We'll change Figure 2 to better show the connection between rainfall in northern South America and the latitudinal position of the ITCZ and illustrate the transport mechanisms of wind and river to the ocean (see new Figure 2 in the supplementary file AC2). We'll also add the 1000, 2300, 3200, and 4800 m contours that are used in defining LR, LMF, UMF, and Páramo, respectively (see new Figure 2, supplementary file AC2).

FLANTUA I.95: The acronym ENSO has been introduced already in line 49.

RESPONSE We'll check all acronyms for necessity and consistency.

FLANTUA I.96: Marchant et al., (2001) is a good example of small-scale climate patterns.

RESPONSE We'll add "(e.g. Marchant et al. 2001, Niemann et al. 2010)"

FLANTUA I.118: Here you specify "the mountains" as the area within Ecuador, while before you talk broadly about the "Northern Andes". For consistency, the Ecuadorean Andes/Cordilleras should be used throughout the paper.

RESPONSE We'll specify Ecuadorean Andes where appropriate; that is at lines 22, 357 and 425. We'll also check the consistency of the capitalisations.

FLANTUA I.127: Palmae = Arecaceae

RESPONSE We'll change Palmae to Arecaceae.

FLANTUA I.141: Santiago river not shown in map?

RESPONSE We'll add the Santiago River on the vegetation map.

FLANTUA I.140-141 & 162: The combination of pollen and fern spores in the pollen

C5

sum is not ideal. In Lowland Forest (< 1000 m) and Lower Montane Forest fern-loaded trees fallen across small rivers shed enormous amounts of spores directly into the water currents (personal observations). Therefore, the proportion of fern spores in the pollen spectra are of a different character than the proportion of pollen, and both components are difficult to compare (see also figures 72-75 in Hooghiemstra et al., 1986).

RESPONSE It makes sense to add the spores to the pollen sum as both are terrestrial derived. The maps of Hooghiemstra et al. 1986 show a clear relation to the distribution of the rain forest on the African continent and the spore abundances in the marine sediments. Dupont & Agwu (1991) showed that the distribution of monolete spores in modern marine sediments compares well with that of *Elaeis guineensis* (Dupont, L.M. and Agwu, C.O.C., 1991. Environmental control of pollen grain distribution patterns in the Gulf of Guinea and offshore NW-Africa. *Geologische Rundschau*, 80: 567-589.) In some marine pollen diagrams (though not in the present study), it is advisable to leave out pollen from typical coastal habitats such as mangroves (Dupont & Weinelt, 1996: Vegetation history of the savannah corridor between the Guinean and the Congolian rain forest during the last 150,000 years. *Vegetation History and Archaeobotany*, 5: 273-292.)

FLANTUA I.143: It would be very useful to have figure 2 show these geographical features such as the Carnegie Ridge and Peru-Chile Trench, and show how pollen would reach the location of the record. 153-154: What is the potential pollen supply by the Humboldt Current? and where could pollen source areas be located?

RESPONSE We'll add bathymetry to vegetation map. Much pollen probably reaches the Carnegie Ridge by means of nepheloid layer transport after reaching the ocean by river discharge. Studies of late Quaternary terrestrial input clearly show the importance of fluvial discharge (González et al., 2006; Ríncon-Martínez et al., 2010). Dominant winds are not favorable for pollen transport to the marine site. The Humboldt Current does not reach the area (we correct that in the new Figure 2, see supplementary file

C6

AC2) and even the Peru-Chile Current flows too far from the coast to be considered an important transport mechanism of pollen grains to our site. Some transport over relative short distances by the Coastal Current (new Figure 2 in supplementary file AC2) is to be expected. We'll add these remarks to the section and the caption of the new Figure 2 (see above, response to line 18).

FLANTUA Furthermore, from this description it's not clear why you are expecting to find signals from the eastern lowlands which constitute the western margin of the Amazon Basin (line 118).

RESPONSE We'll correct the confusing formulation and start the sentence at line 117 with "Ecuador is geographically..." and the next sentence with: "North of Ecuador, the mountains..."

FLANTUA I.156: Avoid starting the sentence with a number. See 191.

RESPONSE The beginning of the paragraph changes anyhow because of the extra samples included: "A total of 68 samples of 10 cm³ volume have been analyzed. For the interval between 301 and 334 m (4.7 and 4.2 Ma),"

FLANTUA I.183 / Table 1: (a) Table 1 shows an effort to group pollen and spore taxa into meaningful ecological groups. A marine pollen record has a wide pollen source area and many taxa listed do have a wide ecological range. The latter makes it difficult to develop clear-cut ecological groups. Páramo: Several 'páramo' taxa also occur in the forest; Upper Montane Forest: Melastomataceae from the UMF also occur abundantly in the páramo; Lowland Forest (LF): is represented by a remarkably low number of taxa; Broad-range taxa: Poaceae indeed have a broad ecological range, but most of it comes from páramo and also dry vegetation in coastal areas and interandean valleys; Asteraceae Tubuliflorae also have a wide range but the bulk is from the páramo; Artemisia seems from Peruvian origin?; Thevetia is indicator of dry conditions rather than a broad range plant; Humid indicators: the following 4 taxa are advised to be omitted from this list: Ranunculaceae (important plant in the puna), Ilex (indeed, also

C7

in wet forest but frequently elsewhere), Myrica (= Morella), and Malpighiaceae (also in savannas).

RESPONSE Indeed, these groupings cannot be 100% sure and some subjectivity is unavoidable. We do not want to include pollen of large families such as Poaceae, Ericaceae, and Asteraceae into the Páramo group, because we try to leave that group as exclusive as possible. If we had included these pollen types into the Páramo group, critics concerning the lack of conclusiveness would have been justified. The group of Humid Indicators is dominated by Cyperaceae pollen and fern spores; thus, the changes you propose have very little impact on the percentage values of the group.

FLANTUA (b) A significant proportion of Lowland Forest (including wet rainforest and dry deciduous forest) and Lower Montane Forest is palynologically 'silent' as many trees are pollinated by insects, beetles, etc. Given the northward flow of the Humboldt Current, and atmospheric circulation in the direction of the coast, I am not surprised that LF is hardly represented by taxa in Table 1. Palms are more abundant in Lower Montane forest (LMF); by moving the Arecaceae from the category LF to LMF, LF is hardly reflected at all. This has consequences for the interpretation and conclusions.

RESPONSE We agree that the representation of the lowland rainforest is weak and is dominated by Polypodiaceae spores. Arecaceae pollen are Wettinia-type from the lowland rainforest (we'll correct the wrong naming in the original supplementary Figure S1) and Socratea distributed in the lowland rainforest from Nicaragua to Bolivia (Marchant et al., 2002). We'll specify the two Arecaceae Wettinia and Socratea in Table 1. We combine Figs. S1-S3 into 1 supplementary figure (see supplementary file AC2). As already stated before, the Humboldt Current does not reach the Carnegie Ridge, but the northbound Coastal Current might have lessened the representation of the lowland forest.

FLANTUA (c) Most of the taxa in the category 'páramo' occur in the ecotone zone of the UMF. Thus the record for 'paramo' as based on the taxa listed in Table 1 may also

C8

reflect the zone with dwarf forest and shrub. (d) In Flantua et al. (2014, figure 7) we explored how altitudinal vegetation zonation is reflected on the basis of GBIF data. We were quite disappointed with the poor altitudinal zonation, possibly explained by a large amount of 'noise' in the GBIF data by using data from a wide geographical region. We concluded that up to date an altitudinal zonation based on expert knowledge from field botanists gives better results: see Groot et al., 2013 (RPP) figure 3).

RESPONSE We group very few taxa in the Páramo and leave out pollen of large families such as Poaceae, Ericaceae and Asteraceae, which other authors (e.g. Hooghiemstra et al., 2006) do include in the Páramo group. Thus, we are very cautious at this point. One of the most important pollen types is *Polylepis/Acaena* (Figure 5) included in the subpáramo by Flantua et al. (2014), which treat sub-, grass-, and superpáramo as one unit. They mention on page 112 of their paper: "The distribution of subpáramo species does not differ from the grasspáramo species; both the nuclei and edges show similar patterns. This justifies the strategy chosen for this analysis, to assess páramo dynamics as a single biome." Therefore, we are convinced that we selected proper indicators for Páramo. The curve of Asteraceae pollen in Figure 5 is only given for comparison. We do not use the Asteraceae record as an indication of Páramo.

FLANTUA I.185: Here, make also reference to Van der Hammen (1974).

RESPONSE We suppose you mean Van der Hammen et al. 1973 (as mentioned in your reference list).

FLANTUA I.188: Which taxa occurred in less than 10% ? A Table showing all identified pollen and spore taxa and their assessment to ecological categories would be helpful.

RESPONSE Table 1 does list ALL taxa as stated in the heading "List of identified pollen and spore taxa. ..." We regret that the figures in the supplement are badly readable. We will amend this in with a new supplementary figure combining Figs S1-S3 (see supplementary file AC2).

C9

FLANTUA I.192: to what refers 'respectively'?

RESPONSE To pollen concentration of 685 grains/cm³ and spore concentration of 465 grains/cm³.

FLANTUA I.194: 26-27% ? Does this relate to a figure?

RESPONSE: Figure 3

FLANTUA I.197: Where is the replacement of *Podocarpus* by *Alnus* shown in a figure?

RESPONSE We add values for *Podocarpus* to Figure 3. We'll replace "whereof the.. *Alnus*" (line 197) with "During the Holocene *Podocarpus* is replaced by *Alnus* as the most abundant upper montane forest tree, although *Podocarpus* was still abundant during the glacial (González et al. 2010)."

FLANTUA I.207: 'The Lowland Rainforest is mainly represented by Polypodiaceae'. However, Polypodiaceae actually occur everywhere and are not a representative of lowland rainforest in particular.

RESPONSE Yes, that is true. However, *Polypodium* is a most common epiphytic on lowland trees (Marchant et al. 2002)

FLANTUA Figure 4: curves are easier to read with a horizontal line at 0%.

RESPONSE We alter the figure and add baselines (see supplementary file AC2).

FLANTUA The elevation indicated for páramo and UFL overlap by 100 m. Is this on purpose?

RESPONSE No, this is a mistake, which we'll correct. We'll take the 3200 meter contour for the transition between Páramo and UMF.

FLANTUA Can your modern samples be shown here as well for comparison?

RESPONSE We make an extra figure (temporally called Fig 4A) comprising samples from the Pleistocene and Holocene. (see Figure 4A in supplementary file AC2)

C10

FLANTUA I.217-237: make reference to the figure where all these changes can be seen.

RESPONSE We'll add "(Fig. 4 and Supplementary Figure)" at line 217.

FLANTUA I.229: 'of the pollen sum' is redundant.

RESPONSE: OK

FLANTUA I.232-233: Podocarpus excluded from the UMF; if I understand well, not from the pollen sum.

RESPONSE: Yes

FLANTUA I.240: 2 out of the 3 species mentioned also occur in the forest (Polylepis, Huperzia). The species mentioned are not a strong indication of the presence of páramo. Lycopodium with foveolate spores is most characteristic of páramo vegetation (Van 't Veer et al., 1992); absence of Lycopodium fov. in the pollen spectra is in support of the view that the present taxa identified as 'reflecting páramo' also are reflecting lowermost páramo and ecotone forest.

RESPONSE We strongly disagree. Your observation that Lycopodium fov would be absent in our record is wrong. Huperzia spores are foveolate (Rincón Baron et al., 2014: Esporogénesis, esporoderma y ornamentación de esporas maduras en Lycopodiaceae in Rev. Biol. Trop., 62: 1161-1195). If you want you may read Huperzia as 'Lycopodium with foveolate spores'. As mentioned above Polylepis is grouped in the subpáramo by yourself (Flantua et al., 2014). Moreover, you also mention: "the distribution of subpáramo species does not differ from the grasspáramo species". Together, with the presence of Jamesonia/Eriosorus spores our argument is valid that Páramo vegetation existed in the Ecuadorian Andes (and maybe beyond) for at least 6 Ma.

FLANTUA I.245: Fig. 5: where is the curve showing páramo vs. montane forest?

RESPONSE: Figure 4 & Figure 7

C11

FLANTUA 'páramo sum' is a confusing term; better to use 'paramo taxa (%)'

RESPONSE OK, we leave out 'sum'. We also changed Fig 5 to show the trends over the full Pliocene and Pleistocene.

FLANTUA I.251-253: difficult to understand why the evidence mentioned is suggesting drier conditions. Please explain more clearly.

RESPONSE Yes, this is not very clear. We'll delete the sentence "This together. . .drier conditions" (line252-253) and rewrite section 4.1 as follows: "In order to better understand the source areas and transport ways of pollen grains to the sediments, we make a comparison of the results of our two Holocene samples with that of another pollen record retrieved from the Carnegie Ridge southeast of Site 1239 (Figure 2) reflecting rainfall and humidity variation of the late Pleistocene (González et al. 2006). Holocene samples of Site 1239 gave similar results showing extensive open vegetation (indicated by pollen of Poaceae, Cyperaceae, Asteraceae) and maximum relative abundance of fern spores although concentration is low González et al., 2006). As also indicated by the elemental ratios, fluvial transport of pollen predominates in this area (González et al., 2006; Rincón-Martínez, 2013). This is understandable as both ocean currents and wind field do not favor transport from Ecuador to Site 1239 (Figure 2)."

FLANTUA I.255: better to show the location of TR 163-38 on the map in Fig. 2.

RESPONSE Yes, we show the position in the new Figure 2 (see supplementary file AC2).

FLANTUA I.267: difficult to understand the claim '(below the forest line)'. How can open grassland below and above the UFL be identified and separated from each other? This seems an over-interpretation of the data.

RESPONSE Apparently, our phrasing has been misunderstood. We'll therefore change "(below the forest line)" to "(apart from Páramo)"

FLANTUA I.270: 'expansion of savannas' ? whereas (line 266) there is a near absence

C12

of open grasslands.

RESPONSE Here, we cite Salzmann et al. (2011) and refer to global vegetation change. To amend the confusion, we'll add "in Africa, for instance"

FLANTUA I.272: 'All altitudinal vegetation belts are already present'. Most possibly correct but not necessarily in its present form. For example, after Quercus had changed the composition of montane forest (LMF and UMF) several LMF taxa were able to reach higher elevations (Hooghiemstra, 1984; Torres et al., 2013). Unfortunately, modern climatological constraints of the lower and upper boundaries of the LMF are insufficiently understood (Hooghiemstra et al., 2012); as a consequence it is difficult to infer climatological change from altitudinal migrations of LMF.

RESPONSE Therefore, we cautiously only remark that "All altitudinal vegetation belts are already present, with varying ratios,"

FLANTUA I.272: 'goes through the most prominent' is unclear, please rephrase.

RESPONSE We'll change the lines 272-273 to: "belts are already present, with varying ratios, and only pollen percentages of lowland rainforest rise from almost absent to 6%."

FLANTUA I.278: 'It is known from other Andean pollen records ...' The comparison made here should be better explained.

I.277: 'show a similar pattern of expansion': what do you mean exactly?, and where can the reader see this expansion?

I.279-282: unclear text, needs rephrasing. For instance, unclear use of 'opposing', what pattern is exactly to be seen in the fig. 5, what is the "more general pattern"?

RESPONSE We'll rephrase lines 274-282 to: "Shifts in the vegetation are driven by various parameters such as temperature, precipitation, CO₂, radiation, and any combination thereof. However, a hint to which parameter has strongest influence on the vegetation might be given by the pattern of expansion and retreat of different vegetation belts."

C13

Hooghiemstra and Ran (1994) indicate that if temperature were the dominant driver of vegetation change, altitudinal shifting of vegetation belts would lead to increase in the representation of one at the cost of another. We do not see such a pattern in our record with the possible exception in zone III where the trends between pollen percentages of Páramo and those of upper montane forest (without Podocarpaceae) are reversed. However, the more general pattern indicates parallel changes in the representation of the forest belts suggesting that not temperature but humidity had the stronger effect on the Pliocene vegetation of Ecuador."

FLANTUA I.287 'the main transport agent for pollen' ; I guess also for spores? Replace here and in the following sentences "El Niño" by ENSO.

RESPONSE In this case, we discuss the warm phase of ENSO that is called El Niño and thus it is better to use that terminology; ENSO comprises all three phases of the oscillation. We'll add: ", the warm phase of ENSO" after El Niño on line 287.

FLANTUA I.292: it would be useful to have a figure that can support this statement on 'lowland rainforest of the coastal plain further north' as it's unclear what "further north" is. Or indicate with lat/long values.

RESPONSE We'll change "further north" into "of Ecuador and western Colombia"

FLANTUA I.294: 'lowland rainforest' is poorly reflected by the taxa listed in Table 1. and as a consequence it is difficult to make a comparison.

RESPONSE We add an extra figure showing the long-term trend of Pliocene and Pleistocene (see Fig. 4A in supplementary file AC2). We'll delete the last sentence of the paragraph.

FLANTUA I.298: Difficult to understand what means 'the development of pollen values is decoupled from'. Needs a better explanation and visualization.

I.300 'eolian' transport is contra to line 140-141.

C14

RESPONSE We'll rephrase lines 298-299: "The trend in pollen percentages of Podocarpaceae divert from that of the other pollen taxa, which may be explained by additional transport of Podocarpaceae pollen by wind. The high pollen production of "
We'll also changed lines 139-143 (see above, response to the comment on line 18).

We'll change lines 305-306 to: "of the easterly trade winds. Increase in trade wind strength at 4.4 Ma would be in line with a shift in the locus of maximum opal accumulation rates in the ocean associated with a shift in nutrient availability (Farrell et al., 1995). Dynamic modelling indicates that stronger easterlies would cause shoaling of the EEP thermocline (Zhang et al., 2012), which took place between 4.8 and 4.0 Ma (Steph et al.," and delete "Another noteworthy oceanographic change occurred at 4.4 Ma in the EEP. Farrell et al. (1995) described a shift in the locus of maximum opal accumulation rates from ODP Site 850 to ODP Site 846 (Galápagos region), caused by a shift in the availability of nutrients, which is possibly related to increased trade wind strength after 4.4 Ma." (lines 314-316)

FLANTUA I.317: 'Besides being influenced by hydrological changes and wind strength' is unclear and needs further explanation.

RESPONSE We'll rephrase lines 317-322 as follows: "Comparing the pollen percentages of Páramo and upper montane forest (Fig. 7) indicates that UMF maxima coincide with Páramo minima and SST maxima at ODP Site 846 (Lawrence et al., 2006). This might be explained by a shift of the upper montane forest to higher altitudes at the cost of the area occupied by Páramo vegetation as a result of higher atmospheric temperatures or increased orographic precipitation in the western Andean Cordillera caused by higher SST and increased evaporation."

FLANTUA I.321: Replace western Andean Cordillera with western Cordillera of Ecuador.

RESPONSE Increase in precipitation would not be restricted to the Cordillera of

C15

Ecuador.

FLANTUA Be consistent throughout the text with Western or western.

RESPONSE We'll stick to "western"

FLANTUA I.324: Sums of upper montane forest = Representation (%) of upper montane forest

RESPONSE We'll change it to "Pollen percentages of"

FLANTUA I.334: better to use the more recent reference '(Hoorn et al., 2010)'

RESPONSE We'll add the reference of Hoorn et al. 2010.

FLANTUA I.333+335: Add 'Ecuador' to Eastern and Western Andean Cordillera

RESPONSE No, the process described would have influenced the Colombian Andes as well.

FLANTUA I.342: In order to use páramo vegetation = In order to use the abundance of páramo vegetation

RESPONSE We'll add "the existence of"

FLANTUA I.343: Replace 'no true páramo endemics' by 'Although no taxa restricted to páramo only were identified. . . .'

RESPONSE: Done

FLANTUA I.347: 'Polylepis is reaching 5000 m in the northern Andes': I guess this refers to Peru and Bolivia and maximum elevations relate to individual trees. In Colombia and Ecuador Polylepis dwarf forest occurs up to 4200-4300 m.

RESPONSE The citation is incorrect. On line 347 is written: "which forms the transition to other forest types and up to 5000 m (Kessler, 2002)." We'll add "in Bolivia"

FLANTUA I.349-351: Perhaps not as present in montane forest and lowland rainforest,

C16

but relatively close to your marine record, you have the presence of several major forest nuclei of seasonally dry tropical forest biome (see Särkinen et al. 2011) and there are a number of different species of Asteraceae in Peruvian seasonally dry tropical forest (see book Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation by T. Pennington & J. Ratter 2006). Could this biome be the source of Asteraceae in your record?

RESPONSE That possibility is exactly why we do not use Asteraceae as an indicator of Páramo.

FLANTUA I.354: 'without changes in composition' is rather meaningless as so few páramo taxa have been identified.

RESPONSE We'll delete "without changes in composition"

FLANTUA I.355: which evidence is fueling this assumption?

RESPONSE The reasoning that mountainous vegetation could grow at higher altitudes during warmer periods.

FLANTUA I.356-357: the weak evidence of páramo does not allow to infer conclusions about the elevation of the Andes.

RESPONSE Our evidence of Páramo is not weak. We show a record of continuous presence since the early Pliocene of pollen of plants (Polylepis, Huperzia, Jamesonia) that grow in subpáramo and páramo and that do not grow at lower altitudes (see also the Figure 4A in supplementary file AC2).

FLANTUA I.362-368: uplift histories of the various areas are confusing here:

RESPONSE Nevertheless, it is necessary to mention the different published opinions. We'll delete "uplift history for the western Cordillera of the Northern Andes and according"

FLANTUA I.362: indeed uplift is older as can be seen in Hoorn et al., 2010. I.364: uplift

C17

of the Central Andes is 60-25 Ma (instead of 10-6 Ma; see Hoorn et al., 2010, Suppl. Info.)

RESPONSE We speak about the major uplift phase.

FLANTUA I.365: Amazon fan = Amazon Fan

RESPONSE: OK

FLANTUA I.365: Which is the first palynological paper to state here "in another recent palynological study.."?

RESPONSE Hoorn et al. (2017) cited at the end of the sentence (as usual).

FLANTUA I.366: The Hoorn et al. 2017 paper suggests but does not provide conclusive evidence that the grass pollen are from páramo as the source area for the Amazon river include also high Andean open vegetation of the puna. This sentence here should be rephrased to not 'oversell' Hoorn et al. 2017 in support of páramo presence.

RESPONSE Hoorn et al. (2017) identified Polylepis and Huperzia (Lycopodium) in sediments of the Amazon Fan. Poaceae and Asteraceae are listed by Hoorn et al (2017) as widely distributed and not included in the group of Páramo indicators. Neither Hoorn et al. nor we claim that grass pollen exclusively comes from the Páramo.

FLANTUA I.377: Amaranthaceae and Thevetia rather are reflecting dry conditions.

RESPONSE Indeed. However, Thevetia occurred with a few exceptions in the earliest Pliocene samples only (older than 4.7 Ma).

FLANTUA I.379: what is the meaning of 'all altitudinal vegetation belts go through simultaneous shifts of expansion and retreat' ?

RESPONSE We'll delete this confusing sentence.

FLANTUA I.382: Add space before the 3.

RESPONSE: OK

C18

FLANTUA I.385: Better explain 'parallel expansion and retreat of all vegetation belts'. For the last 20 ka we have learned that little goes parallel (see Hooghiemstra and Van der Hammen, 2004).

RESPONSE We'll rephrase the sentence as follows "Our record does not show increased representation of one vegetation belt at the cost of another indicating that altitudinal shifts were not extensive and moisture availability might have been an important driver of Pliocene vegetation change." and start the next sentence with "Changes in humidity could..."

FLANTUA I.419: Eastern Cordillera reached = Eastern Cordillera of Colombia reached

RESPONSE: Done

FLANTUA I.421: 'argue for a rapid rise of the region since 4-6 Ma' ; This is outdated and should be 30-5 Ma (see Hoorn et al., 2010 Suppl. Info.)

RESPONSE Indeed. We'll change "argue" into "argued"

FLANTUA I.425: 'Our pollen record from the páramo shows' This conclusion seems unwarranted as the evidence for páramo vegetation is weak and also could reflect ecotone forest and/or other biomes.

RESPONSE We can only repeat that we use very specific Páramo indicators and do NOT use the record of broad range taxa such as Asteraceae and Poaceae.

FLANTUA I.435: On which evidence is this sentence based?

RESPONSE This has been extensively discussed in the previous section.

FLANTUA I.440: Conclusion 2 is difficult to understand: when? a shift to what?

RESPONSE We'll rephrase as follows: "The most prominent shift recorded is an increase in the representation of the lowland rainforest."

FLANTUA I.441: Higher representation of Podocarpaceae is interpreted as evidence

C19

of more intense trade winds. However, this is not necessarily the case as pollen record Funza09 (Torres et al., 2013, figure 10) shows that Podocarpus is more abundant during several intervals of Pleistocene time, potentially also leading to high representation in the marine sediments.

RESPONSE Our argumentation is not based on the abundance of Podocarpaceae pollen but on the divergence between the trends in pollen percentages of Podocarpaceae and those of other pollen and spores (see Section 4.2.2)

FLANTUA I.447-448: The presence of páramo is weakly supported by evidence; the inferred altitude of the Ecuadorian (?) Andes is speculative as a consequence

RESPONSE We can only repeat that we use very specific Páramo indicators and do NOT use the record of broad range taxa such as Asteraceae and Poaceae. . FLANTUA

I.449-450: Better to refer to more recent literature in which the uplift of the Northern Andes has been set back in time already.

RESPONSE We'll rephrase: "We present new paleobotanical evidence indicating an earlier development of Páramo vegetation than..."

FLANTUA I.564: Reference Montes et al. 2015 is incomplete.

RESPONSE We'll correct the reference of Montes and also the missing parts of the references of Ríncón-Martínez 2013, Sánchez-Baracaldo, 2004 (American Fern Journal 94(3):126-142. 2004), Flantua et al. 2014.

FLANTUA Fig. S1: To which degree modern core top samples are comparable to the pre-Quaternary samples? Are mechanisms of pollen transport comparable? Some re-marks about this issue are missing.

RESPONSE All transport mechanisms were already in place during the Pliocene. However, some enhancement of SE trade winds might have been captured by the Podocarpus pollen record, which is discussed in Section 4.2.2.

C20

FLANTUA Fig. S2: % sum páramo = páramo (place the word 'percentage' in the figure caption) :also for other taxa

RESPONSE: OK

FLANTUA Fig. S3: Mention in the caption 'Pollen percentage diagram' and omit all % indications on top of the pollen diagram. And: Myrica = Morella

RESPONSE Figure S3 will be replaced (see supplementary figure in supplementary file AC2). Myrica is corrected to Morella

FLANTUA IN CONCLUSION: The biomes 'páramo' and 'lowland rainforest' are hardly reflected by characteristic pollen and spore taxa. Several taxa now classified as 'broad range taxa' could be shifted to 'páramo' but with the same restriction that these taxa also could reflect uppermost montane forest (ecotone forest).

RESPONSE First you tell us to include Poaceae, Asteraceae, and Ericaceae in the Páramo group and subsequently you argue that these families are too widely distributed to indicate Páramo vegetation. We deliberately did not use broad-range families as indicator for Páramo, but used specific Páramo indicators such as Polylepis-Acaena pollen and spores of Lycopodium fov (Huperzia) and Jamesonia/Eriosorus. We thus have a strong record of early Pliocene Páramo vegetation in the Ecuadorian Andes. You try to refute our claim by erroneously stating or implying that our Páramo indicators would be based on broad range families such as Asteraceae, Ericaceae and Poaceae.

FLANTUA In marine pollen records changing proportions of pollen taxa / ecological groups may reflect vegetation change and / or changes in pollen transport. In the present manuscript the latter is hardly/not considered (This remark also relates to the suggestions for improvement of Fig. 2).

RESPONSE We'll expand the section about transport source areas of pollen and spores (Section 1.1.2., see response to comment on line 18). We consider the ef-

C21

fects of transport mechanisms as we discuss different transport mechanisms in the case of the Podocarpus record (Section 4.2.2). Fig. 2 has been changed to better illustrate the possible transport routes (see supplementary file AC2).

FLANTUA Integration of terrestrial and marine proxies is a powerful tool to maximize conclusions. The comparison with model output has broadened the scope of this paper but – apart from speculation - has not generated an incremental step forwards.

RESPONSE Based on our data, we clearly take position about southward shift of the Pliocene ITCZ pro data and contra modelling results (Lines 380-400) and discuss several aspects of the problem (Lines 401-428). We protest against the disqualifying phrase "apart from speculation".

FLANTUA Pollen zones in Fig. S3 are not expressive and the interpretation in terms of environmental change is not convincing. The presented pollen evidence does not allow a full support of the suggested conclusions of this paper. Analysing a much longer interval has the potential to strengthen conclusions, but the regional setting will remain poor to obtain convincing evidence.

RESPONSE We agree that Figs S1-S3 are barely readable and we replace them with a new supplementary figure combining Fig. S1, S2 and S3 (see supplementary file AC2). The pollen zones are supported by the cluster analysis (CONISS), which is shown in the first panel of the supplementary figure. We originally used the coring gap as a zone boundary, which we agree is not correct. Therefore, we now only use the CONISS clustering to define the pollen zones. This results in the extension of pollen zone II downward (see supplementary figure in file AC2). We'll adapt the description and further carry out all necessary corrections. However, the shift in the boundary between pollen zones I and II does not affect the discussion or the conclusions. We make an extra figure (see Fig 4A in supplementary file AC2) showing at low resolution the trends in Pliocene and Pleistocene.

A detailed study of the upper Pliocene is in preparation.

C22

ADDITIONAL REFERENCES

Marchant, R., Behling, H., Berrio, J.C., Cleef, A., Duivenvoorden, J., Hooghiemstra, H., Kuhry, P., Melief, B., Van Geel, B., Van der Hammen, Th., Van Reenen, G., Wille, M., 2001. Mid- to Late-Holocene pollen-based biome reconstructions for Colombia. *Quaternary Science Reviews*, 20: 1289-1308.

Niemann, H., Brunschöm, C., Behling, H., 2010. Vegetation/modern pollen rain relationship along an altitudinal transect between 1920 and 3185 m a.s.l. in the Podocarpus National Park region, southeastern Ecuadorian Andes. *Review of Palaeobotany and Palynology*, 159: 69-80.

Wijninga, V.M., 1996. Palynology and palaeobotany of the Early Pliocene section Río Frío 17 (Cordillera Oriental, Colombia): biostratigraphical and chronostratigraphical implications. *Review of Palaeobotany and Palynology*, 92: 329-350.

Wijninga, V.M. and Kuhry, P., 1990. A Pliocene Flora from the Subachoque Calley (Cordillera Oriental, Colombia). *Review of Palaeobotany and Palynology*, 62: 249-290.
Additional references:

Interactive comment on *Clim. Past Discuss.*, <https://doi.org/10.5194/cp-2017-129>, 2017.

Interactive comment on “Early Pliocene vegetation and hydrology changes in western equatorial South America” by Friederike Grimmer et al.

C. Hoorn (Referee)

m.c.hoorn@uva.nl

Received and published: 21 December 2017

Paper: Early Pliocene vegetation and hydrology changes in western equatorial South America by Grimmer et al.

Reviewer Carina Hoorn

Summary The purpose of the paper is to establish the direction of shift of the ITCZ following the closure of the Central American Seaway (CAS) and uplift of the northern Andes. The paper comprises a palynological study of sediments from the interval between 4.7 and 4.2 Ma of the appropriately situated ODP core 1239A. The specific aims are to reconstruct vegetation, climate and topography in this region throughout this time interval. The conclusion is that an (already) high Andean landscape existed

C1

at the time, and that both vegetation and landscape during this interval match with a scenario corresponding to a southward shift of the ITCZ. Fluctuations of the ENSO are also considered. The results are in accordance with other paleoceanographic data in the region.

Main comments:

There is a shortage of continuous records from the Pliocene in the eastern Pacific that reflect hydrological and climatic change in the region. This paper aims to fill this gap. However, the dataset makes it hard to see the big changes that one would expect from the text. If possible the dataset should be extended with additional data to which are referred in the text.

• The interaction of Andean uplift, closure of the CAS, shifting ITCZ and ENSO altogether make it quite a daunting task to interpret the palynological diagram and assign changes to specific causes. The case is clearly made and looked at from all angles. Question: Is there a chance that some of the subtle changes in the diagram can be related to the Pliocene uplift pulses in the Andes and related atmospheric changes? Such pulses are postulated in tectonic reconstructions (e.g. Anderson et al., 2015, Geosphere) and are mentioned by authors in the paragraph starting at line 464.

• The new dataset further confirm that a high topography (Anderson et al., 2015) and paramo (Bermudez et al., 2015 in Basin Research; Hoorn et al., 2017 in Global & Planetary Change) was in place at least since the early Pliocene. It might be worthwhile highlighting the regional character of this condition?

Note that modern type precipitation patterns are likely to have been in place already from middle Miocene onwards (see Kaandorp et al., 2006; Hoorn et al., 2010; Barnes et al., 2012) and this would have required a significant orographic barrier. A high Andes might go as far back as the mid-Miocene, however, first evidence for a paramo is now set as latest Miocene to early Pliocene. Lines 406-407 could be reconsidered in this context.

C2

â€” The elemental concentrations analysis needs to be better introduced and is currently rather hidden and makes a surprise first appearance in the methods section. In methods also explain why this is a useful additional technique. Part of the text in section 4.3 (line 360 onwards) could be moved to the introduction to explain approach.

â€” The discussion of the Holocene samples in relation to the Pliocene seems a bit ambivalent and does not form a very good guideline to better understand the new results.

â€” Lines from 313: A rather crucial line comes up here and reads as follows: “unpublished data from the earliest Pliocene show that the percentage of lowland rainforest before 4.7 Ma was very low”. The evidence that is presented seems rather subtle and perhaps not iconic for an important vegetation & climate change. The authors allude to data of the earliest Pliocene, which they say strengthen their case. However, they are not visible. If these data belong to the authors it might be timely to include them here (or a selection of them) and make a more compelling case.

â€” A map with the scenarios for the changing ITCZ would be welcome. Instead this could also be added to figure 1.

Minor comments:

â€” In line 465 Hoorn et al. 2010 are listed as backing up a rapid rise of the region since 4– 6 Ma, However we suggest in the mid-Miocene the Andes must have already been high with further uplift at a later stage.

â€” The writing style at places can be somewhat convolute and could do with rephrasing. A suggestion for the opening sentence would be: “The progressive closure of the Central American Seaway (CAS) and the uplift of the northern Andes profoundly re-organized early Pliocene ocean and atmospheric circulation in the Eastern Equatorial Pacific (EEP).”

Interactive comment on Clim. Past Discuss., <https://doi.org/10.5194/cp-2017-129>, 2017.

Interactive comment on “Early Pliocene vegetation and hydrology changes in western equatorial South America” by Friederike Grimmer et al.

Friederike Grimmer et al.

fgrimmer@marum.de

Received and published: 26 June 2018

HOORN Summary The purpose of the paper is to establish the direction of shift of the ITCZ following the closure of the Central American Seaway (CAS) and uplift of the northern Andes. The paper comprises a palynological study of sediments from the interval between 4.7 and 4.2 Ma of the appropriately situated ODP core 1239A. The specific aims are to reconstruct vegetation, climate and topography in this region throughout this time interval. The conclusion is that an (already) high Andean landscape existed at the time, and that both vegetation and landscape during this interval match with a scenario corresponding to a southward shift of the ITCZ. Fluctuations of the ENSO are also considered. The results are in accordance with other paleoceanographic data in the region.

C1

Main comments: There is a shortage of continuous records from the Pliocene in the eastern Pacific that reflect hydrological and climatic change in the region. This paper aims to fill this gap. However, the dataset makes it hard to see the big changes that one would expect from the text. If possible the dataset should be extended with additional data to which are referred in the text.

RESPONSE We emphasize in the text that the changes within the analyzed time window are rather small (e.g. line 20 “stable, permanently humid conditions”; line 271 “During the early Pliocene, no profound changes in the vegetation occur”). We prepare an extra figure (Fig 4A in supplementary file) showing both the data discussed in the manuscript and the data of a pilot study to show the long-term trends. It should be kept in mind that the age model for the period between 5 and 6 Ma is based on shipboard data and less detailed. **We will adapt the text accordingly and include: “Percentages of humidity indicators hint to slightly drier conditions at the beginning of the Pliocene. A trend towards higher palynomorph concentrations is found for the period from 6 to 2 Ma. Grass pollen percentages remain low indicating mainly closed forest at altitudes below the Páramo. Representation of lowland rainforest was low around 4.7 Ma, increased by 4.5 Ma, declined again to low levels around 3.5 Ma, and rose to remain at higher levels during the Pleistocene. Continuous presence of pollen and spores from the Páramo indicates that the northern Andes had reached high altitudes in Ecuador before the Pliocene.”**

HOORN The interaction of Andean uplift, closure of the CAS, shifting ITCZ and ENSO altogether make it quite a daunting task to interpret the palynological diagram and assign changes to specific causes. The case is clearly made and looked at from all angles. Question: Is there a chance that some of the subtle changes in the diagram can be related to the Pliocene uplift pulses in the Andes and related atmospheric changes? Such pulses are postulated in tectonic reconstructions (e.g. Anderson et al., 2015, Geosphere) and are mentioned by authors in the paragraph starting at line 464.

RESPONSE We do not understand this question. We cannot find a paper of Anderson

C2

et al. in *Geosphere*, vol. 11 (2015). We therefore assume that meant is the paper of Anderson et al. in *GSA Bulletin* that we cite on line 422. However, this paper does not discuss pulses of uplift but that the uplift since 7.6 Ma was more gradual than hypothesized by, for instance, Hooghiemstra et al. (2006).

HOORN The new dataset further confirm that a high topography (Anderson et al., 2015) and paramo (Bermudez et al., 2015 in *Basin Research*; Hoorn et al., 2017 in *Global & Planetary Change*) was in place at least since the early Pliocene. It might be worthwhile highlighting the regional character of this condition?

RESPONSE To highlight the regional character, we'll specify Ecuadorean Andes at line 425: "that the Ecuadorean Andes must have already reached close to modern elevations by the early Pliocene": "in line with inferences of Hoorn et al. (2017) and Bermúdez et al. (2015)." (line 425-6). We'll add the reference of Berúmdez et al. to the list. At line 420 we'll add: "Moreover, phases of major uplift might have strongly differed regionally." We'll also specify Ecuadorean Andes at lines 22 and 357.

HOORN Note that modern type precipitation patterns are likely to have been in place already from middle Miocene onwards (see Kaandorp et al., 2006; Hoorn et al., 2010; Barnes et al., 2012) and this would have required a significant orographic barrier. A high Andes might go as far back as the mid-Miocene, however, first evidence for a paramo is now set as latest Miocene to early Pliocene. Lines 406-407 could be reconsidered in this context.

RESPONSE We'll insert "which probably were more or less in place (Kaandorp et al., 2006; Hoorn et al., 2010)," in line 407 after "Possibly these oceanic reorganizations did not directly trigger modifications of the atmospheric circulation," and add the extra reference to the list.

HOORN The elemental concentrations analysis needs to be better introduced and is currently rather hidden and makes a surprise first appearance in the methods section. In methods also explain why this is a useful additional technique. Part of the text in

C3

section 4.3 (line 360 onwards) could be moved to the introduction to explain approach.

RESPONSE We are reluctant to shift section 4.3 to the Introduction as it discusses the interpretation of the elemental ratio results. Instead, we'll shift the section to the beginning of the discussion (new section 4.1 see at next point). To satisfy the valid objection, we'll mention the use of elemental ratios at the end of the Introduction (line 75) inserting: "We also use elemental ratios to estimate variations in fluvial terrestrial input (Ríncon-Martínez et al. 2010)."

HOORN The discussion of the Holocene samples in relation to the Pliocene seems a bit ambivalent and does not form a very good guideline to better understand the new results.

RESPONSE To better explain what guidelines we use to interpret the Pliocene record, we'll make the following changes. We change Fig. 2 (supplementary file) and add to Section 1.1.2 two paragraphs replacing lines 139-143:

"Ríncon-Martínez et al. (2010) showed that the terrigenous sediment supply at ODP Site 1239 during Pleistocene interglacials is mainly fluvial and input of terrestrial material drop to low amounts during the drier glacial stages. Also transport of pollen and spores to the ocean is mainly fluvial (González et al., 2010). High rates of orographic precipitation characterize the western part of equatorial South America. These heavy rains quickly wash out any pollen that might be in the air and result in large discharge by the Ecuadoran Rivers (Fig. 2). Esmeraldas and Santiago Rivers mainly drain the northern coastal plain of Ecuador, and the southern coastal plain is drained by several smaller rivers, which end in the Guayas River. Moreover, the predominantly westerly winds (Fig. 2) are not favorable for eolian pollen dispersal to the ocean. Nevertheless, some transport by SE trade winds is possible and should be taken into account.

"After reaching the ocean pollen and spores might pass the Peru-Chile Trench, which is quite narrow along the Carnegie Ridge, by means of nepheloid layers at subsurface depths. Some northward transport from the Bay of Guayaquil by the Coastal Current

C4

(Fig. 2) is likely. However, the Peru-Chile Current flows too far from the coast to have strong influence on pollen and spore dispersal. We consider western Ecuador, northernmost Peru and southwestern Colombia the main source areas of pollen and spores in sediments of ODP Site 1239.”

We'll switch sections 3.1 and 3.2 to emphasize the function of the Holocene analysis as a tool for interpretation. We add values for Podocarpus to Figure 3 (see supplementary file). We'll replace “whereof the... Alnus” (line 197) with “During the Holocene Podocarpus is replaced by Alnus as the most abundant upper montane forest tree, although Podocarpus was still abundant during the glacial (González et al. 2010).”

We'll rewrite section 4.1 and put it behind the discussion about the elemental ratios consequently becoming section 4.2. We'll open the rewritten section as follows: “In order to better understand the source areas and transport ways of pollen grains to the sediments, we make a comparison of the results of our two Holocene samples with that of another pollen record retrieved from the Carnegie Ridge southeast of Site 1239 (Figure 2) reflecting rainfall and humidity variation of the late Pleistocene (González et al. 2006). Holocene samples of Site 1239 gave similar results showing extensive open vegetation (indicated by pollen of Poaceae, Cyperaceae, Asteraceae) and maximum relative abundance of fern spores although concentration is low (González et al., 2006). As also indicated by the elemental ratios, fluvial transport of pollen predominates in this area (González et al., 2006; Ríncon-Martínez, 2013). This is understandable as both ocean currents and wind field do not favor transport from Ecuador to Site 1239 (Figure 2).”

HOORN Lines from 313: A rather crucial line comes up here and reads as follows: “unpublished data from the earliest Pliocene show that the percentage of lowland rainforest before 4.7 Ma was very low”. The evidence that is presented seems rather subtle and perhaps not iconic for an important vegetation & climate change. The authors allude to data of the earliest Pliocene, which they say strengthen their case. However, they are not visible. If these data belong to the authors it might be timely to include

C5

them here (or a selection of them) and make a more compelling case.

RESPONSE We'll introduce a new figure (Fig 4A in supplementary file) with the selected results of the pilot study (see also response above) illustrating the low rainforest pollen percentages prior to 4.7 Ma and, more importantly, the continuously higher values after 3 Ma. We'll correct and precise the description accordingly.

HOORN A map with the scenarios for the changing ITCZ would be welcome. Instead this could also be added to figure 1.

RESPONSE We'll change Figure 2 (which we assume is referred to) to show the wind-field together with the resulting precipitation during boreal summer (July), because this is the rainy season in the region. This should illustrate the correspondence of the summer rains in northern South America with the present northern limit of the ITCZ. Furthermore, we'll include a panel with summer SST combined with main ocean currents. The adapted figure is shown separately in the supplementary file. This, together with the revision of Section 1.1.2, should also illustrate the ineffectiveness of transport mechanisms other than fluvial discharge by the Guayas and Esmeraldas Rivers.

HOORN Minor comments: In line 465 Hoorn et al. 2010 are listed as backing up a rapid rise of the region since 4–6 Ma, However we suggest in the mid-Miocene the Andes must have already been high with further uplift at a later stage.

RESPONSE Sorry about that. We'll delete Hoorn et al. (2010) from the list and add it later in the paragraph in the altered sentence: “Possibly these oceanic reorganizations did not directly trigger modifications of the atmospheric circulation, which probably were more or less in place (Kaandorp et al., 2006; Hoorn et al., 2010), but critical periods of uplift influencing atmospheric circulation might have occurred earlier.” (see also above).

HOORN The writing style at places can be somewhat convolute and could do with rephrasing. A suggestion for the opening sentence would be: “The progressive closure of the Central American Seaway (CAS) and the uplift of the northern Andes profoundly

C6

reorganized early Pliocene ocean and atmospheric circulation in the Eastern Equatorial Pacific (EEP).“

RESPONSE We'll do our best and adopt your suggestion for the opening sentence.

ADDITIONAL REFERENCES

Bermúdez, M.A., Hoorn, C., Bernet, M., Carillo, E., Van der Beek, P.A., Garver, J.I., Mora, J.L., and Mehrkian, K.: The detrital record of late-Miocene to Pliocene surface uplift and exhumation of the Venezuelan Andes in the Maracaibo and Barinas foreland basins, *Basin Research*, 29, Supplement 1, 370-395, 2017.

Kaandorp, R.J.G., Wesselingh, F.O., and Vonhof, H.B.: Ecological implications from geochemical records of Miocene Western Amazonian bivalves, *Journal of South American Earth Sciences*, 21, 54-74, 2006.

Interactive comment on *Clim. Past Discuss.*, <https://doi.org/10.5194/cp-2017-129>, 2017.

Interactive comment on “Early Pliocene vegetation and hydrology changes in western equatorial South America” by Friederike Grimmer et al.

J. TIAN (Referee)

tianjun@tongji.edu.cn

Received and published: 19 March 2018

This study generated new vegetation and climate record between 4.7 and 4.2 Ma by pollen analysis of 46 samples from ODP Site 1239A, which is located in the East Equatorial Pacific, a place suitable for investigating the precipitation-related fluvial runoff changes in northwestern South America, thus good for monitoring the past movement of the ITCZ. A major aim of this study is to clarify a mismatch about the ITCZ shift in the early Pliocene between the proxy records and the model simulation, that most proxy data supports a southward shift whereas numerical modelling suggests a northward shift in response to Central American Seaway closure and Andean uplift. Generally, this study fills the blank of well dated hydrological record of the early Pliocene in this region by pollen and spores studies from marine sediment.

C1

Generally, I agree with the comments posted by the other three referees and won't repeat it. Here are some minor suggestions, which I think should help the readers to better understand this research if considered.

Age model. How did the authors establish the age model for the study interval of Site 1239? From Tiedemann et al. (2007)? Why not add the benthic $\delta^{18}\text{O}$ record to the figures and sign labels of Marine Isotope Stages? You cannot just cite a reference to get all the necessary things done.

Continuity of the record. Since other palynological studies of the region have been conducted for the mid-Pliocene to the Holocene, why not combine those records with the new record of the early Pliocene? Are they from the same marine core? The new record depends on 46 samples to cover the time interval of 4.7-4.2 Ma, with an average time resolution of 11 Kyr. In such a relatively short period and with a relatively low time resolution, the authors still recognize four major steps of the vegetation changes, and claim that all the vegetation belts as explained in Figures 3 and showed in Figure 4 display synchronous increase/decrease for each stage. If carefully examining figure 4, the features of the variability of the vegetation belts just constrainedly match those described in the text. The referee RC1 also pointed it out. Increasing the time resolution such as doubling, and filling the hiatus between cores 35X and 36X of Hole 1239A (there should be also vegetation change in this interval), something very different probably could happen. Also as indicated by Referee RC1, the unpublished data which is so important to support the author's conclusion of a low percentage of lowland rainforest before 4.7 Ma should be put together with the presented record of this manuscript. I believe that all readers with interests for the ITCZ shift in the early Pliocene would like to see a continuous record since the early Pliocene rather than a segmented record in such a narrow period.

About permanent El Niño, closure of Central American Seaway and Andean uplift. My suggestion is weakening the discussion on these comprehensive topics but focusing on its significance in indicating the hydrological changes. The new pollen records are not

C2

strong evidences to support the so ambitious conclusions in the present manuscript.

Interactive comment on Clim. Past Discuss., <https://doi.org/10.5194/cp-2017-129>, 2017.

Interactive comment on “Early Pliocene vegetation and hydrology changes in western equatorial South America” by Friederike Grimmer et al.

Friederike Grimmer et al.

fgrimmer@marum.de

Received and published: 26 June 2018

TIAN This study generated new vegetation and climate record between 4.7 and 4.2 Ma by pollen analysis of 46 samples from ODP Site 1239A, which is located in the East Equatorial Pacific, a place suitable for investigating the precipitation-related fluvial runoff changes in northwestern South America, thus good for monitoring the past movement of the ITCZ. A major aim of this study is to clarify a mismatch about the ITCZ shift in the early Pliocene between the proxy records and the model simulation, that most proxy data supports a southward shift whereas numerical modelling suggests a northward shift in response to Central American Seaway closure and Andean uplift. Generally, this study fills the blank of well dated hydrological record of the early Pliocene in this region by pollen and spores studies from marine sediment. Generally,

C1

I agree with the comments posted by the other three referees and won't repeat it. Here are some minor suggestions, which I think should help the readers to better understand this research if considered.

Age model. How did the authors establish the age model for the study interval of Site 1239? From Tiedemann et al. (2007)? Why not add the benthic d18O record to the figures and sign labels of Marine Isotope Stages? You cannot just cite a reference to get all the necessary things done.

RESPONSE We'll add the d18OC.wuellerstorfi data of Tiedemann et al. 2007 to Figure 4 (see supplementary file AC2). However, in this part of the Pliocene the fluctuations in the stable oxygen values are small. Also in the stable oxygen data a gap is present around 4.5 Ma, because they have only been measured on sediments of Hole A (same as the pollen). In the results section, we will specify that we used the Tiedemann et al. (2007) age model.

TIAN Continuity of the record. Since other palynological studies of the region have been conducted for the mid-Pliocene to the Holocene, why not combine those records with the new record of the early Pliocene? Are they from the same marine core? The new record depends on 46 samples to cover the time interval of 4.7-4.2 Ma, with an average time resolution of 11 Kyr. In such a relatively short period and with a relatively low time resolution, the authors still recognize four major steps of the vegetation changes, and claim that all the vegetation belts as explained in Figures 3 and showed in Figure 4 display synchronous increase/decrease for each stage. If carefully examining figure 4, the features of the variability of the vegetation belts just constrainedly match those described in the text. The referee RC1 also pointed it out. Increasing the time resolution such as doubling, and filling the hiatus between cores 35X and 36X of Hole 1239A (there should be also vegetation change in this interval), something very different probably could happen. Also as indicated by Referee RC1, the unpublished data which is so important to support the author's conclusion of a low percentage of lowland rainforest before 4.7 Ma should be put together with the presented record of

C2

this manuscript. I believe that all readers with interests for the ITCZ shift in the early Pliocene would like to see a continuous record since the early Pliocene rather than a segmented record in such a narrow period.

RESPONSE We think that 11 kyr sample resolution is not too bad for the Early Pliocene. Please, keep in mind that palynological analysis is very time consuming and needs a palynologist well trained in the specifics of the pollen flora under discussion.

We originally put a zone boundary at the coring gap, which in hindsight was unfortunate and, more important, not backed up by the cluster analysis. The CONISS cluster analysis groups samples from below and above the coring gap together suggesting no fundamental trend changes took place during the period in between as also indicated by the XRF-record. We correct this in the new version. Filling the coring gap would take several months of analysis and might not be strictly necessary.

To put the data in a better perspective and to present a more continuous record, we add analyses from the low-resolution pilot study, as also asked for by Carina Hoorn (Figure 4A in supplementary file AC2). We might draw your attention to the long-term development of the lowland forest.

To our knowledge the only published marine pollen diagrams from the region are those of ODP 677 and TR163-38 covering the past 40 and 15ka, respectively (González et al. 2006), and M772-056 covering the past 11ka (Seillès et al., 2016). There is overlap with the top three samples. We wrote on lines 255-257: "A Holocene pollen record from nearby core TR 163-38 has high similarity to the core top samples in its youngest part, showing increased open vegetation (Poaceae, Cyperaceae, Asteraceae), low percentages of Rhizophora, maximum percentages of fern spores, and low pollen and spores concentrations (González et al., 2006)." To which we'll add: "A pollen record closer to the coast - from the Bay of Guayaquil - also indicate relative open vegetation and drier mid- to late Holocene conditions (Seillès et al. 2015) as does the record of ODP Site 677 from the deep basin northwest of Carnegie Ridge (González et al. 2006)."

C3

Detailed analyses for the mid-Pliocene are in progress and are hopefully published (at least submitted) next year. However, this work will focus on the mid-Piacenzian warm Period and on the intensification of the Northern Hemisphere Glaciations. Those are very different themes and beyond the scope of this paper.

TIAN About permanent Elño, closure of Central American Seaway and Andean uplift. My suggestion is weakening the discussion on these comprehensive topics but focusing on its significance in indicating the hydrological changes. The new pollen records are not strong evidences to support the so ambitious conclusions in the present manuscript.

RESPONSE We agree that the changes in the vegetation coupled to changes in hydrology is the core of our paper. We try to look at the hydrological changes from all perspectives as acknowledged by Carina Hoorn. We think that it is important to do so, because so many globally important drivers influence the hydrology of the region. We also are convinced that our Páramo record can be used as an argument that at least the Ecuadoran Andes were already high in the Early Pliocene (see also the responses to Flantua & Hooghiemstra). We'll check the phrasing of the discussion

Interactive comment on Clim. Past Discuss., <https://doi.org/10.5194/cp-2017-129>, 2017.

C4

Interactive comment on “Early Pliocene vegetation and hydrology changes in western equatorial South America” by Friederike Grimmer et al.

Friederike Grimmer et al.

fgrimmer@marum.de

Received and published: 26 June 2018

The comment was uploaded in the form of a supplement:
<https://www.clim-past-discuss.net/cp-2017-129/cp-2017-129-AC2-supplement.pdf>

Interactive comment on Clim. Past Discuss., <https://doi.org/10.5194/cp-2017-129>, 2017.

Figure 2. Modern climate (boreal summer) and vegetation and core site positions of ODP Sites 677, 846, 851, 1000, 1239, 1241, Trident core TR163-38, and M772-056 mentioned in the text. **A.** Long-term monthly July precipitation in mm/day (CPC) and wind field (NCEP). July is the middle of the rainy season in northern South America, when the ITCZ is at its northern boreal summer position. Salinity estimates for the Caribbean indicate a position of the ITZC further north during the Pliocene. Direction of wind is not favorable for wind transport of pollen and spores to ODP Site 1239. **B.** Long-term monthly July sea surface temperatures (NODC), surface and subsurface currents of the eastern equatorial Pacific (Mix et al. 2003). NECC, North Equatorial Countercurrent; SEC, South Equatorial Current; PCC, Peru-Chile Current (continuation of the Humboldt Current); CC, Coastal Current; EUC, Equatorial Undercurrent; GUC, Gunther Undercurrent. **C.** Contours, bathymetry (ETOPO1), main rivers in Ecuador, and vegetation. Transport of pollen and spores in the ocean over the Peru-Chile Trench, which is very narrow east of the Carnegie Ridge, probably takes place in nepheloid layers. Páramo vegetation is found between 3200 and 4800 m, upper montane Andean forest (UMF) grows between 1000 and 2300 m, sub-Andean lower montane forest (LMF) between 1000 and 2300 m, and lowland forest (LR) below 1000m. The distribution of desert and xeric shrubs in northern Peru, drier broad-leaved forest, flooded grasslands, and mangroves in Ecuador and Colombia is denoted in different colors (see legend, WWF). Source areas of pollen and spores in sediments of ODP Site 1239 are sought in western Ecuador, northwestern Peru, and southwestern Colombia (see text).

References:

Mix, Tiedemann, Blum et al. 2003: Init Report ODP, leg 202.

World Wildlife Fund (WWF). <https://www.worldwildlife.org/ecoregions/> (retrieved November 2017)

National centers for Environmental Information (NOAA):

- CPC Merged Analysis of Precipitation. <http://www.cdc.noaa.gov/cdc/data.cmap.html> (retrieved February 2008)
- ETOPO1. <https://maps.ngdc.noaa.gov/viewers/wcs-client/> (retrieved June 2018)
- NCEP reanalysis data (meridional and zonal wind). <http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.derived.html> (retrieved January 2010)
- NODC (Levitus) World Ocean Atlas. <http://www.esrl.noaa.gov/psd/data/gridded/data.nodc.woa94.html> (retrieved March 2010)

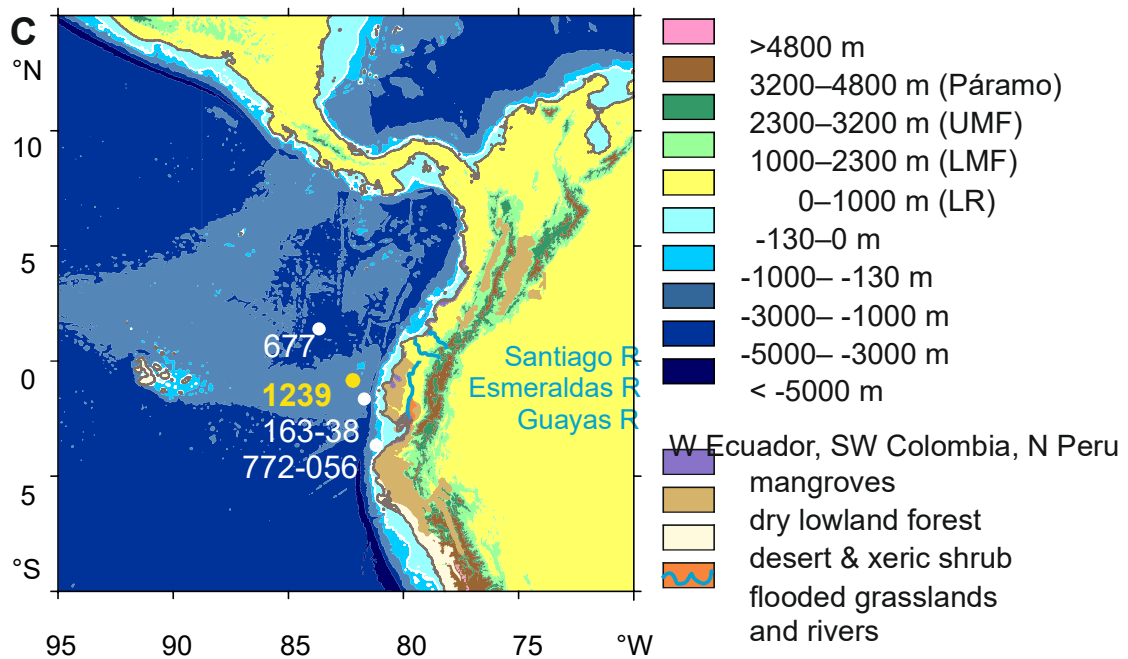
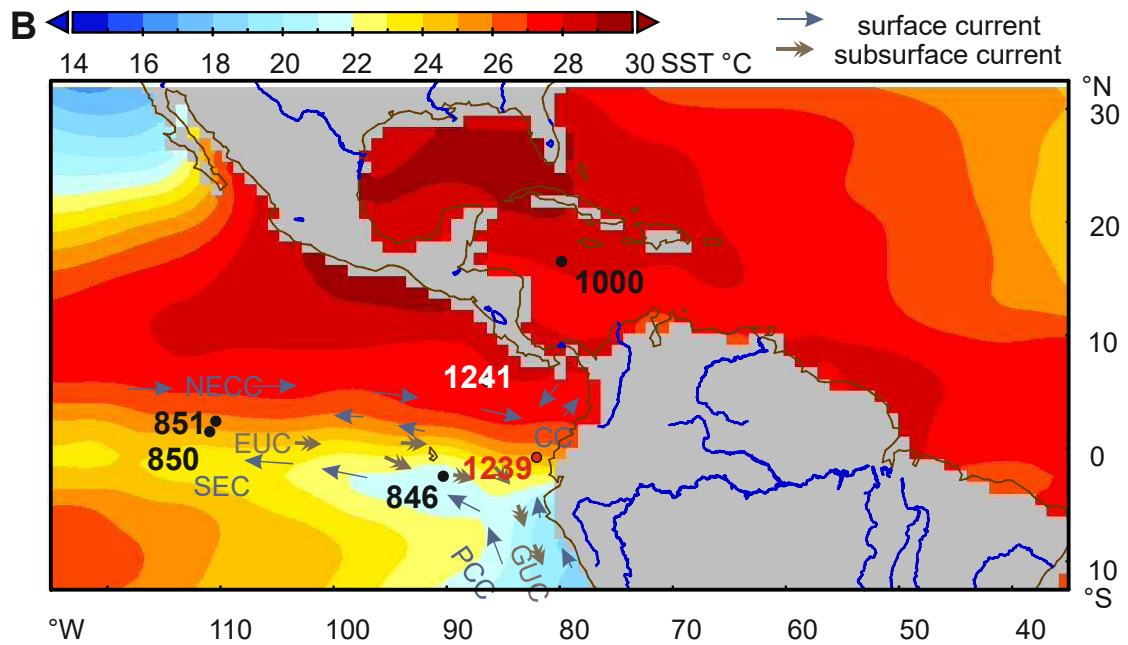
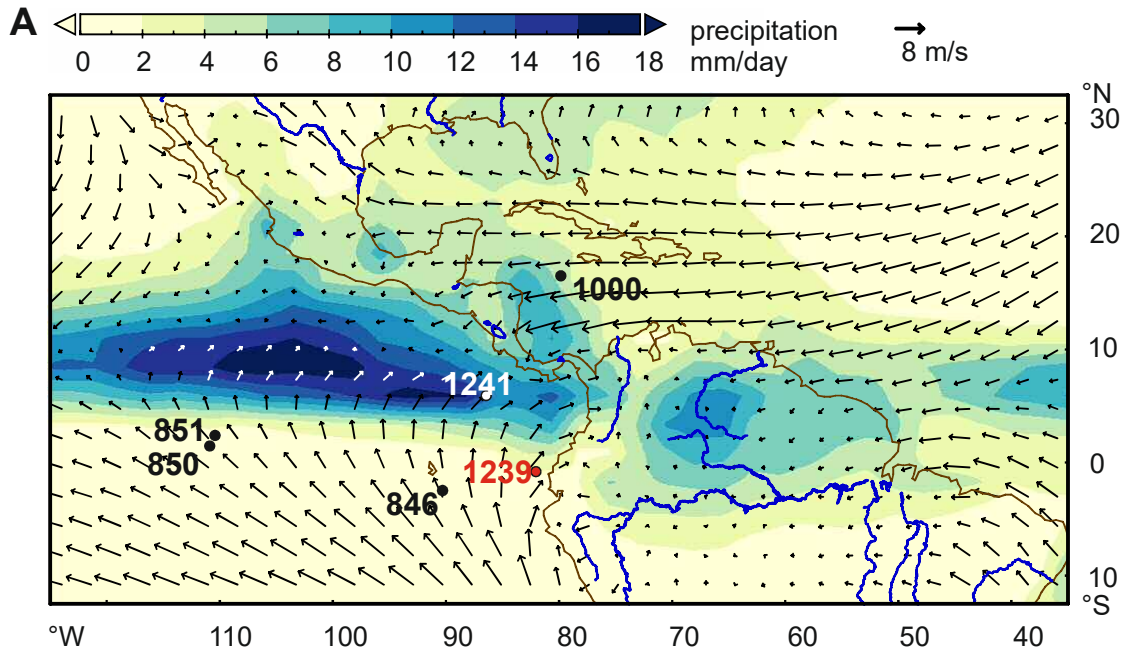


Figure 3. Comparison of the palynomorph percentages (based on total pollen and spores) of Podocarpaceae and the different vegetation belts between 2 Holocene samples (black) and Pliocene samples between 4.7-4.2 Ma (box-whisker plots).

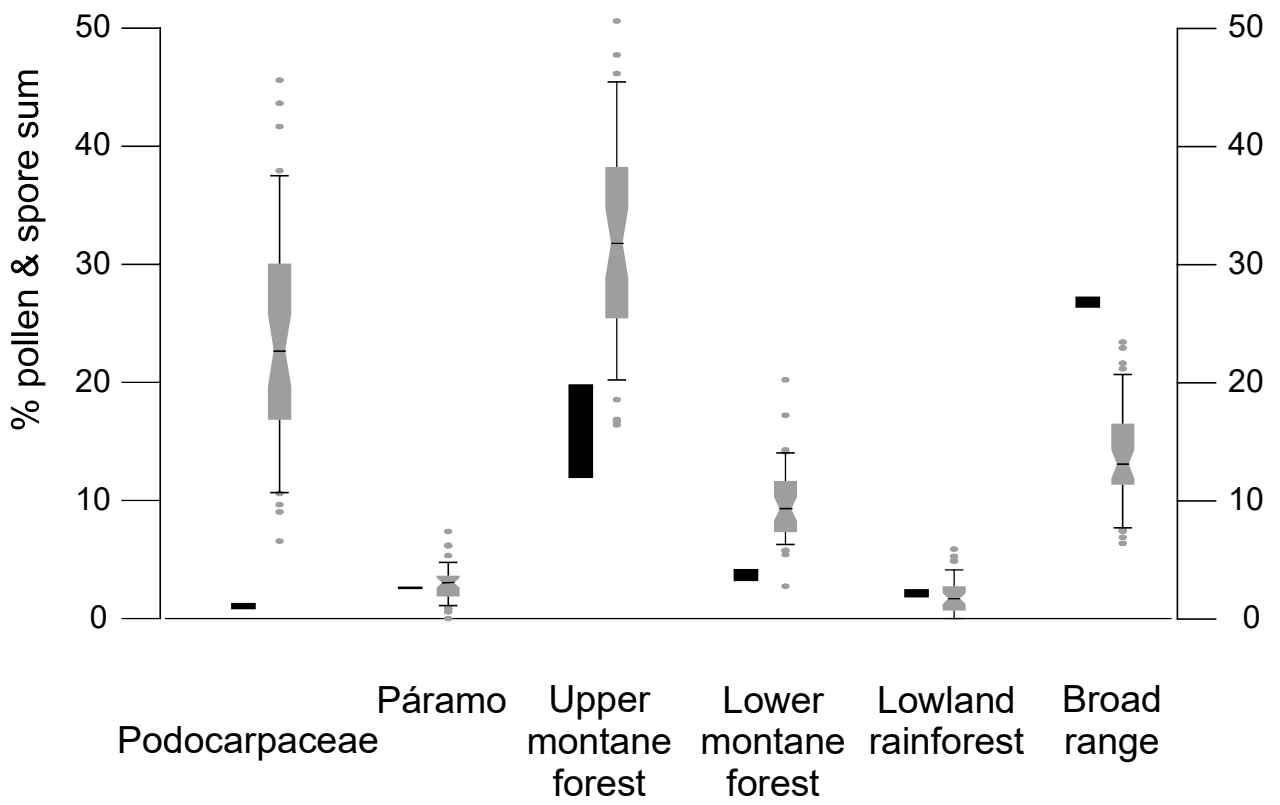


Figure 4A (extra figure). Pliocene and Pleistocene palynomorph percentages (based on the total of pollen and spores) of ODP Hole 1239A for three vegetation belts, humidity indicators, grass pollen and pollen and spore concentration per ml. 95% confidence intervals as grey bars after Maher (1972).

Additional Results. Percentages of humidity indicators hint to slightly drier conditions at the beginning of the Pliocene. A trend towards higher palynomorph concentrations is found for the period from 6 to 2 Ma. Grass pollen percentages remain low indicating mainly closed forest at altitudes below the Páramo. Representation of lowland rainforest was low around 4.7 Ma, increased by 4.5 Ma, declined again to low levels around 3.5 Ma, and rose to remain at higher levels during the Pleistocene. Continuous presence of pollen and spores from the Páramo indicates that the northern Andes had reached high altitudes in Ecuador before the Pliocene.

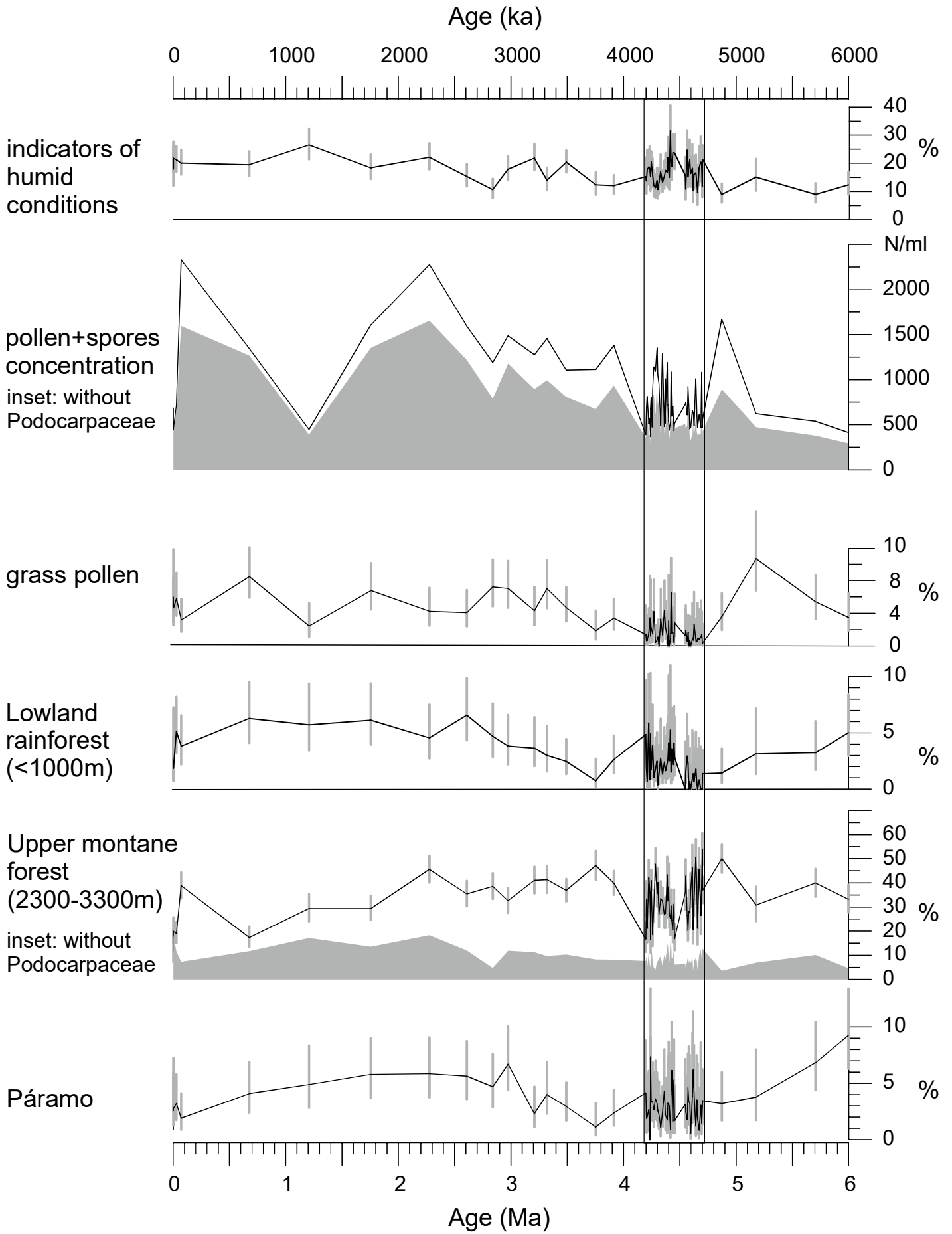


Figure 4. Palynomorph percentages of ODP Hole 1239A for the four vegetation belts and other groups from 4.7 to 4.2 Ma. Grey shading represents the 95% confidence intervals (after Maher, 1972). Vertical black lines delimit the pollen zones. At the top stable oxygen isotopes of the benthic foraminifer *C. wuellerstorfi* (Tiedemann et al., 2007) of ODP Hole 1239A, marine isotope stages (MIS), and elemental ratios of Fe/K from Holes 1239A and 1239B. Ages are from Tiedemann et al. (2007). A coring gap is present in Hole 1239A between 4.45 and 4.55 Ma.

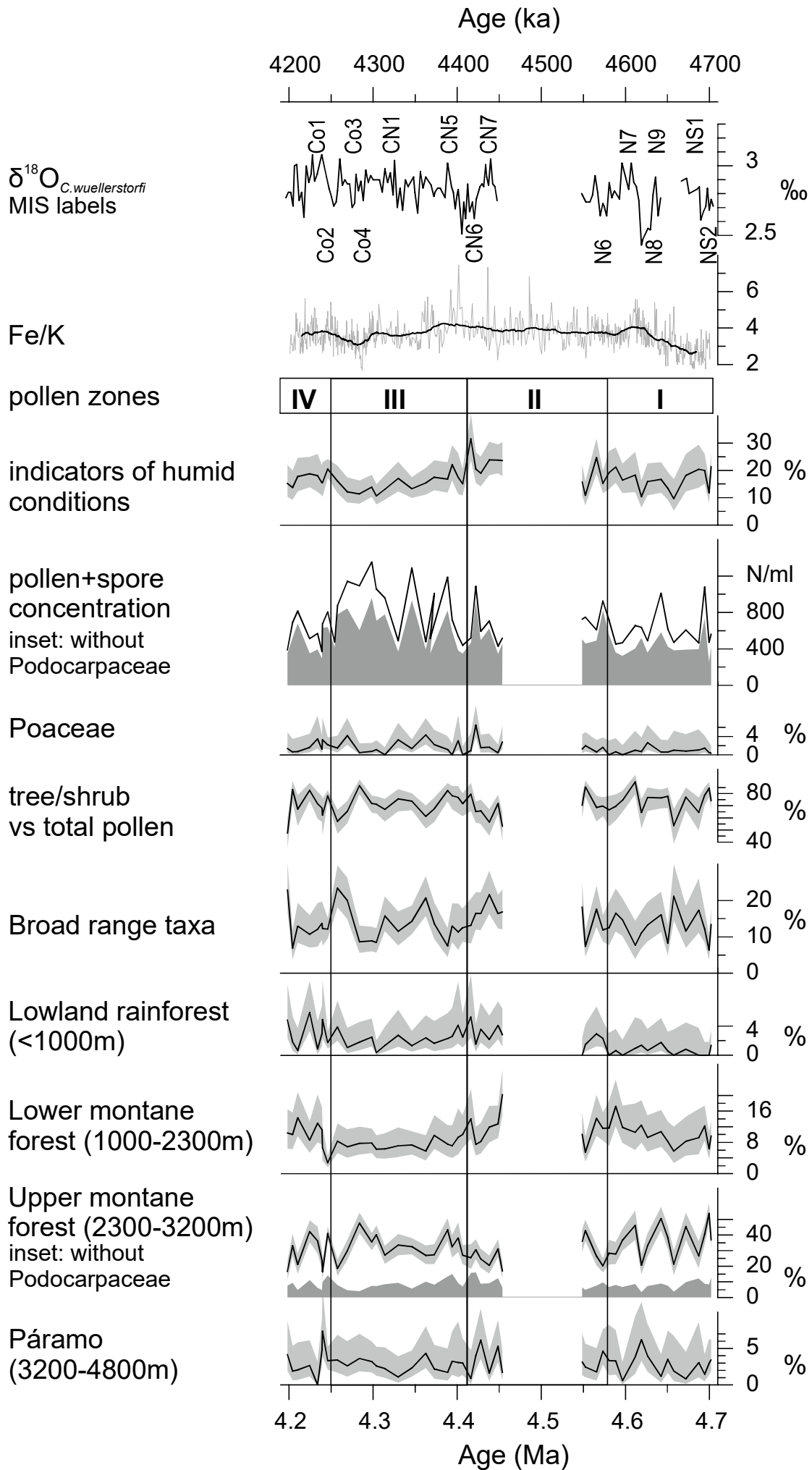


Figure 5. Palynomorph percentages of Páramo indicators and Asteraceae Tubuliflorae (excluding Ambrosia/Xanthium T) of the past 6 Ma indicating the presence of Páramo vegetation at least since the late Miocene. 95% confidence intervals (grey bars) after Maler (1972). Ages after Tiedemann et al. (2007).

Age (ka)

0 1000 2000 3000 4000 5000 6000

Polylepis/
Acaena

10

0

Huperzia

10

0

Jamesonia/
Eriosorus

10

0

Páramo

10

0

Asteraceae
Tubuliflorae

20

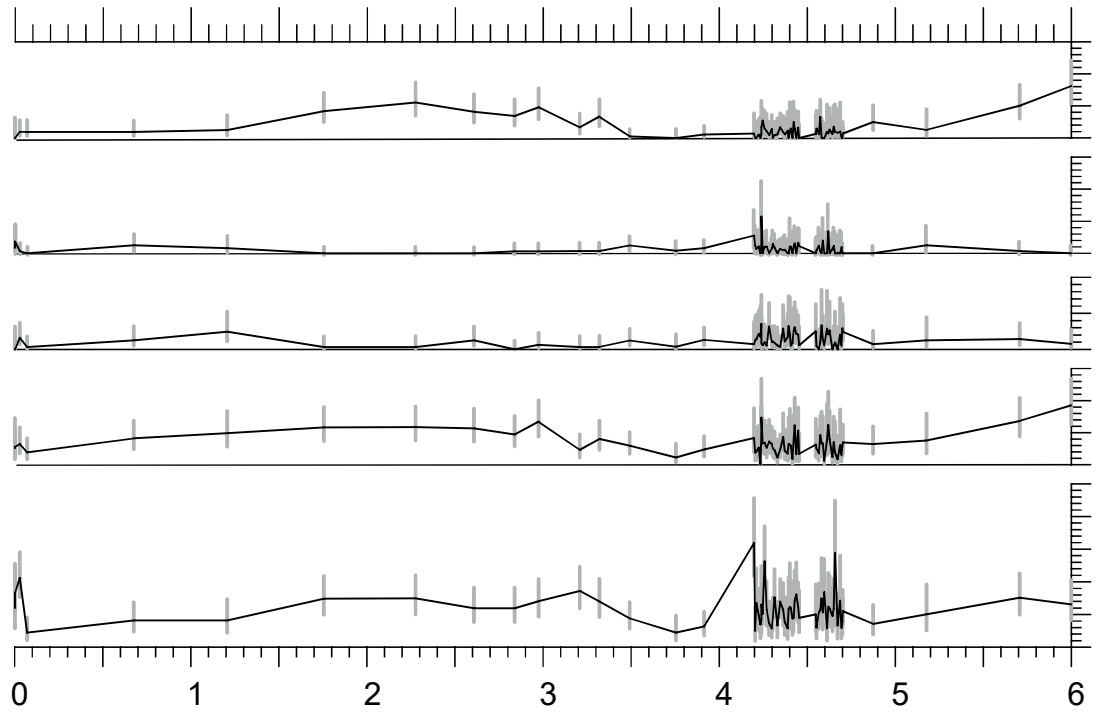
10

0

% pollen + spores

0 1 2 3 4 5 6

Age (Ma)

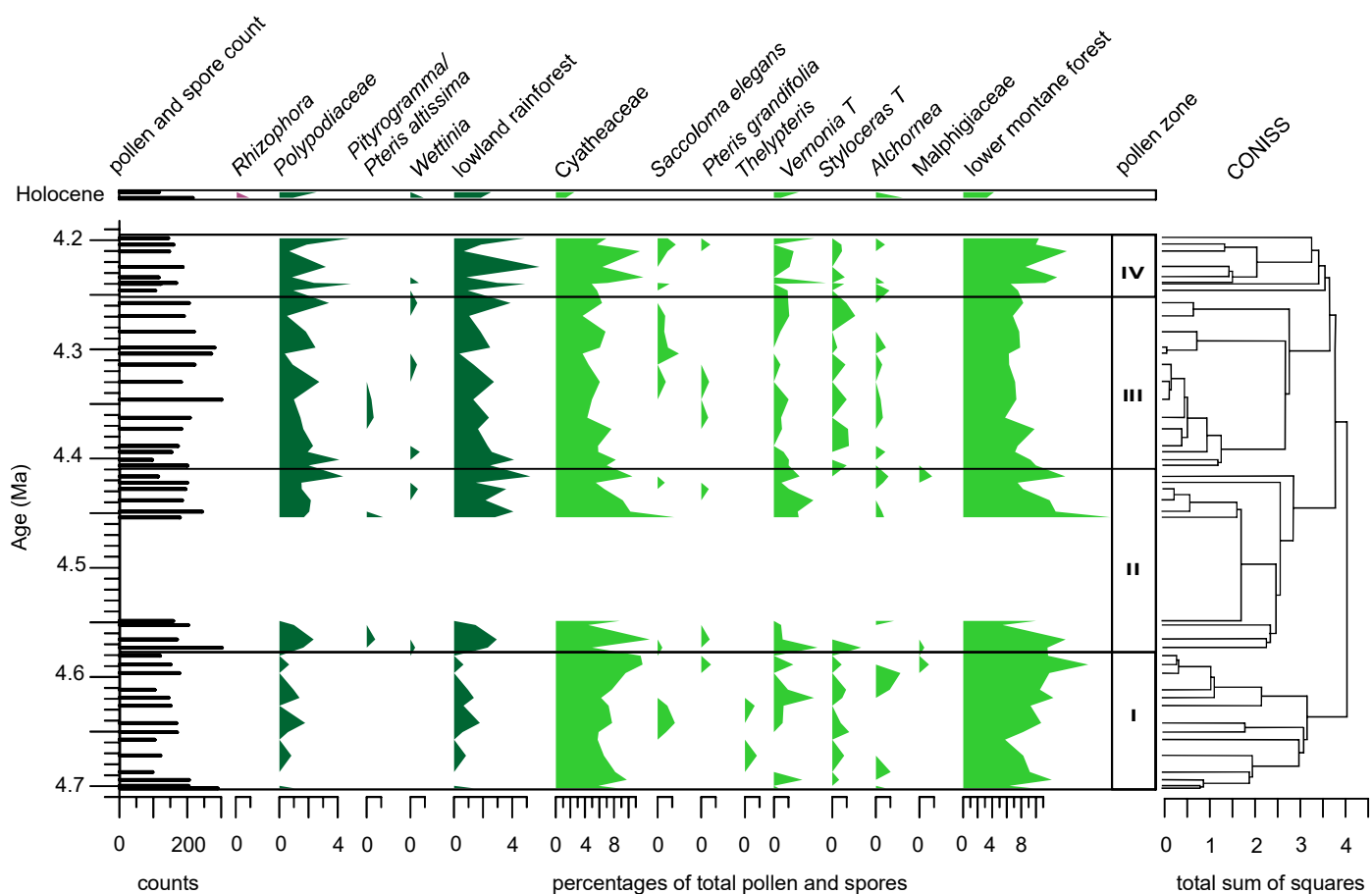


1 Table 1: List of identified pollen and spore taxa in marine ODP Holes 1239A (Pliocene samples) and 1239B (core top samples,
2 taxa in grey occurred only in core top samples) and grouping according to their main ecological affinity (Flantua et al., 2014;
3 Marchant et al., 2002).
4

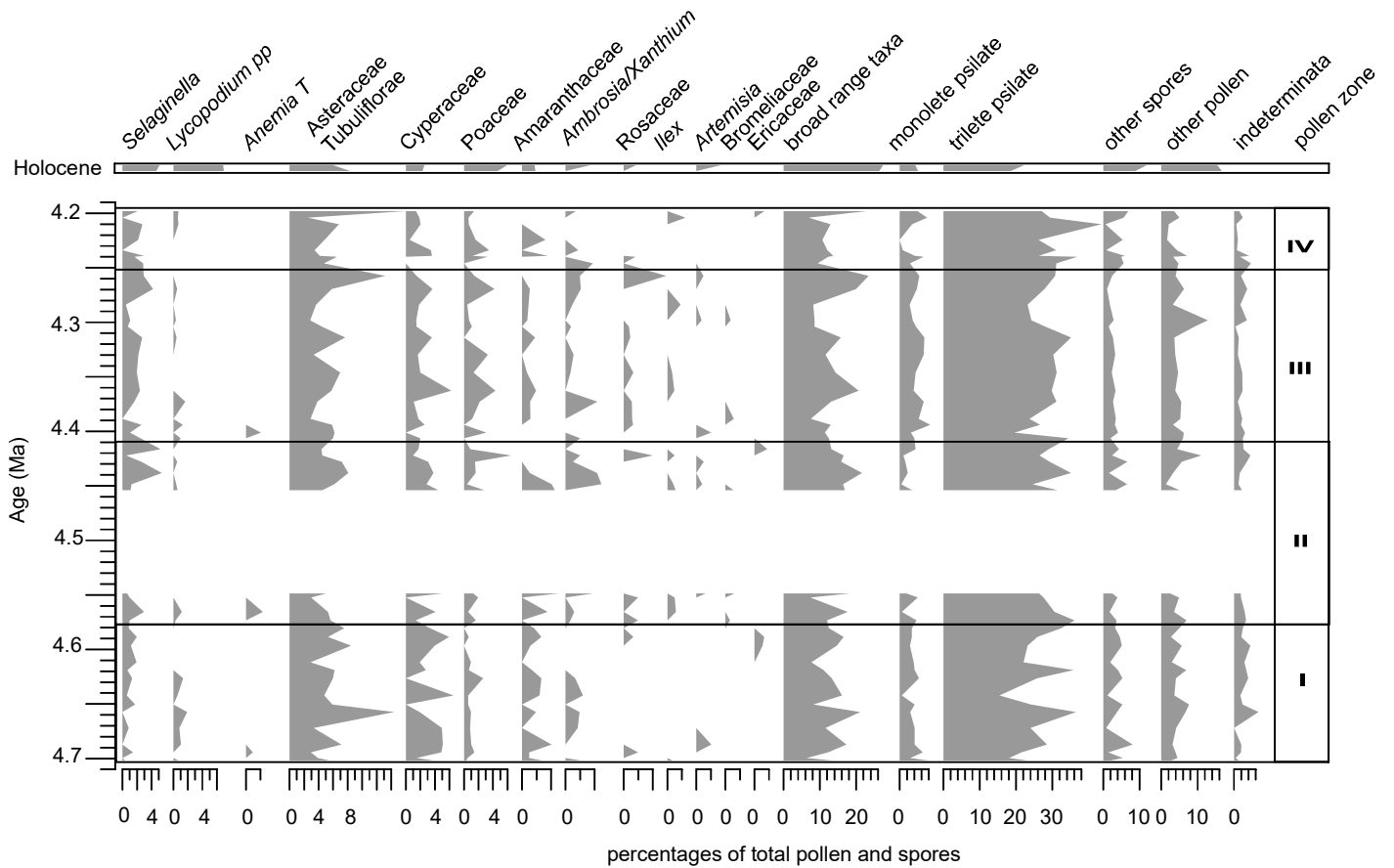
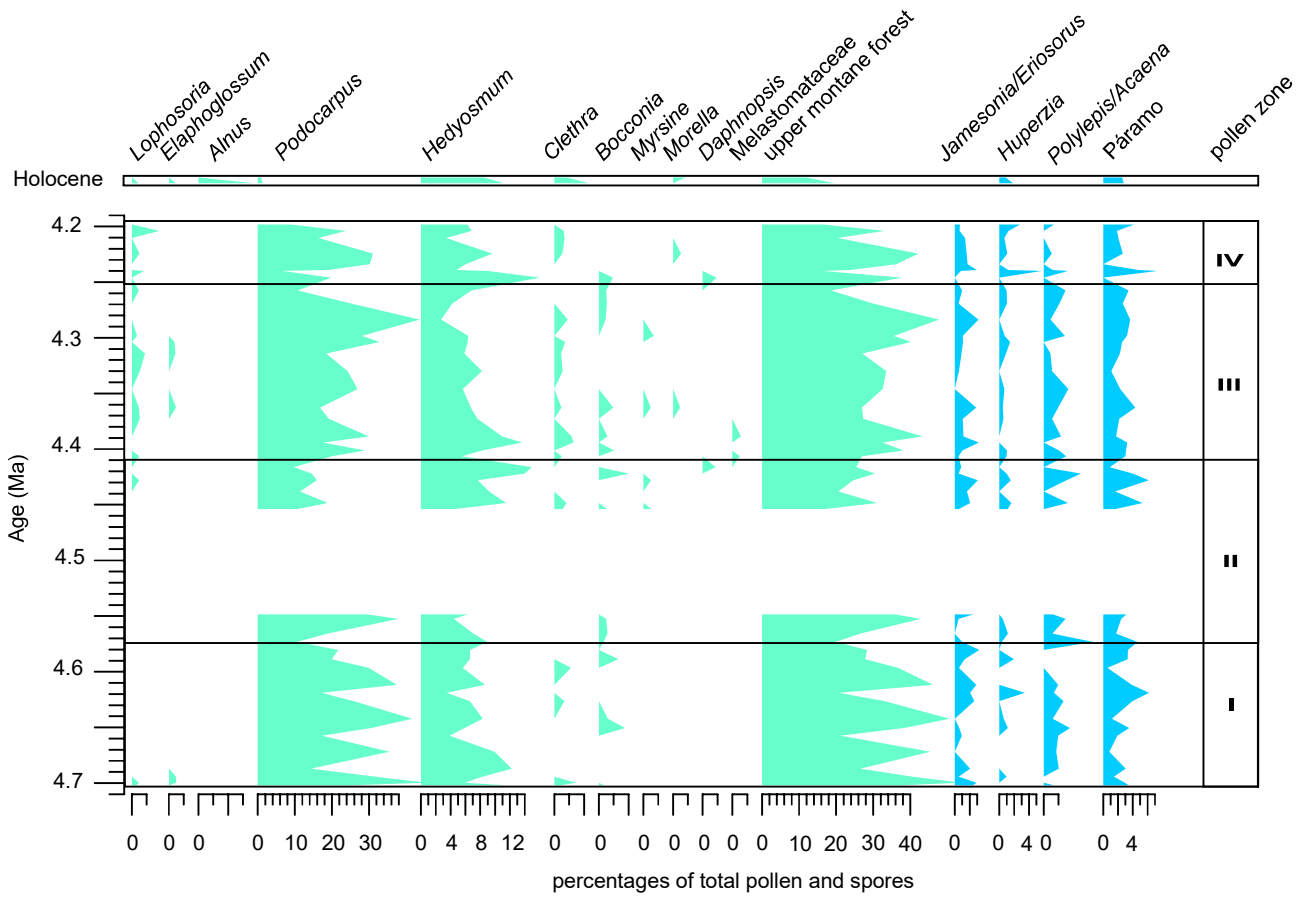
Páramo	Upper montane forest	Lower montane forest	Lowland rainforest	Broad range taxa	Humid indicators
<i>Polylepis/Acaena</i>	Podocarpaceae	Urticaceae/ Moraceae	<i>Wettinia</i>	Poaceae	Cyperaceae
<i>Jamesonia/Eriosorus</i>	<i>Hedyosmum</i>	<i>Erythrina</i>	<i>Socratea</i>	Cyperaceae	<i>Ranunculus</i>
<i>Huperzia</i>	<i>Clethra</i>	<i>Alchornea</i>	Polypodiaceae	Tubuliflorae (Asteraceae)	<i>Hedyosmum</i>
<i>Ranunculus</i>	<i>Morella</i>	<i>Styloceras T</i>	<i>Pityrogramma/ Pteris altissima T</i>	Amaranthaceae	<i>Ilex</i>
<i>Draba</i>	Acanthaceae	Malpighiaceae		Rosaceae	<i>Pachira</i>
<i>Sisyrinchium</i>	Melastomataceae	Cyatheaceae		<i>Ambrosia/ Xanthium</i>	<i>Morella</i>
<i>Cystopteris diaphana T</i>	<i>Daphnopsis</i>	<i>Vernonia T</i>		Ericaceae	Malpighiaceae
	<i>Bocconia</i>	<i>Pteris grandifolia T</i>		<i>Artemisia</i>	Cyatheaceae
	<i>Myrsine</i>	<i>Pteris podophylla T</i>		<i>Ilex</i>	<i>Selaginella</i>
	<i>Lophosoria</i>	<i>Saccoloma elegans T</i>		<i>Thevetia</i>	<i>Pityrogramma/ Pteris altissima T</i>
	<i>Elaphoglossum</i>	<i>Thelypteris</i>		<i>Salacia</i>	<i>Hymenophyllum T</i>
	<i>Hypolepis hostilis T</i>	<i>Ctenitis subincisa T</i>		Bromeliaceae	<i>Thelypteris</i>
	<i>Grammitis</i>			Malvaceae	<i>Ctenitis subincisa T</i>
	<i>Dodonaea viscosa</i>			Euphorbiaceae	<i>Alnus</i>
	<i>Alnus</i>			<i>Liliaceae</i>	<i>Cystopteris diaphana T</i>
				Lycopodiaceae excl. <i>Huperzia</i> <i>Selaginella</i>	
				<i>Hymenophyllum T</i>	
				<i>Calandrinia</i>	

5

6



Supplementary figure. Pollen percentage diagram against age (Tiedemann et al., 2007), with total counts, percentages of single taxa and groups, pollen zones, CONISS clusters based on the curves of single pollen taxa. On top two samples from the Holocene. Minor ticks denote 1%, major ticks 2%, unless stated differently. This panel shows pollen and spore taxa from mangrove, lowland rainforest and lower montane forest. Panels on the next page show the pollen percentages for taxa from the upper montane forest, páramo, and broad range taxa.



Supplementary figure (continued)

Early Pliocene vegetation and hydrology changes in western equatorial South America

Friederike Grimmer¹, Lydie Dupont¹, Frank Lamy², Gerlinde Jung¹, Catalina González³, Gerold Wefer¹

¹MARUM – Center for Marine Environmental Sciences, University of Bremen, Leobener Str. 8, 28359 Bremen, Germany

²Alfred-Wegener-Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany

³Department of Biological Sciences, Universidad de los Andes, Cra. 1 #18a-12, Bogotá, Colombia

Correspondence to: Friederike Grimmer (fgrimmer@marum.de)

Abstract. During the early Pliocene, two major tectonic events triggered a profound reorganization of ocean and atmospheric circulation in the Eastern Equatorial Pacific (EEP), the Caribbean Sea, and on adjacent land masses: the progressive closure of the Central American Seaway (CAS) and the uplift of the northern Andes. These affected amongst others the mean latitudinal position of the Intertropical Convergence Zone (ITCZ). The direction of an ITCZ shift however is still debated, as numeric modelling results and paleoceanographic data indicate shifts in opposite directions. To provide new insights into this debate, an independent hydrological record of western equatorial South America was generated. Vegetation and climate of this area were reconstructed by pollen analysis of 46 samples from marine sediments ~~core~~ [of ODP Hole 1239A](#) from the EEP comprising the interval between 4.7 and 4.2 Ma. The study site is sensitive to latitudinal ITCZ shifts insofar as a southward (northward) shift would result in increased (decreased) precipitation over Ecuador. The presented pollen record comprises representatives from five ecological groups: lowland rainforest, lower montane forest, upper montane forest, páramo, and broad range taxa. A broad tropical rainforest coverage persisted in the study area throughout the early Pliocene, without significant open vegetation ~~below the forest line~~ [beyond the páramo](#). Between 4.7 and 4.42 Ma, humidity increases, reaching its peak around 4.42 Ma, and slightly decreasing again afterwards. The stable, permanently humid conditions are rather in agreement with paleoceanographic data indicating a southward shift of the ITCZ, possibly in response to CAS closure. The presence of páramo vegetation indicates that the ~~Western Cordillera of the northern~~ [Ecuadorian](#) Andes had already reached considerable elevation by the early Pliocene. Future studies could extend the hydrological record of the region further back into the late Miocene to see if a more profound atmospheric response to tectonic changes occurred earlier.

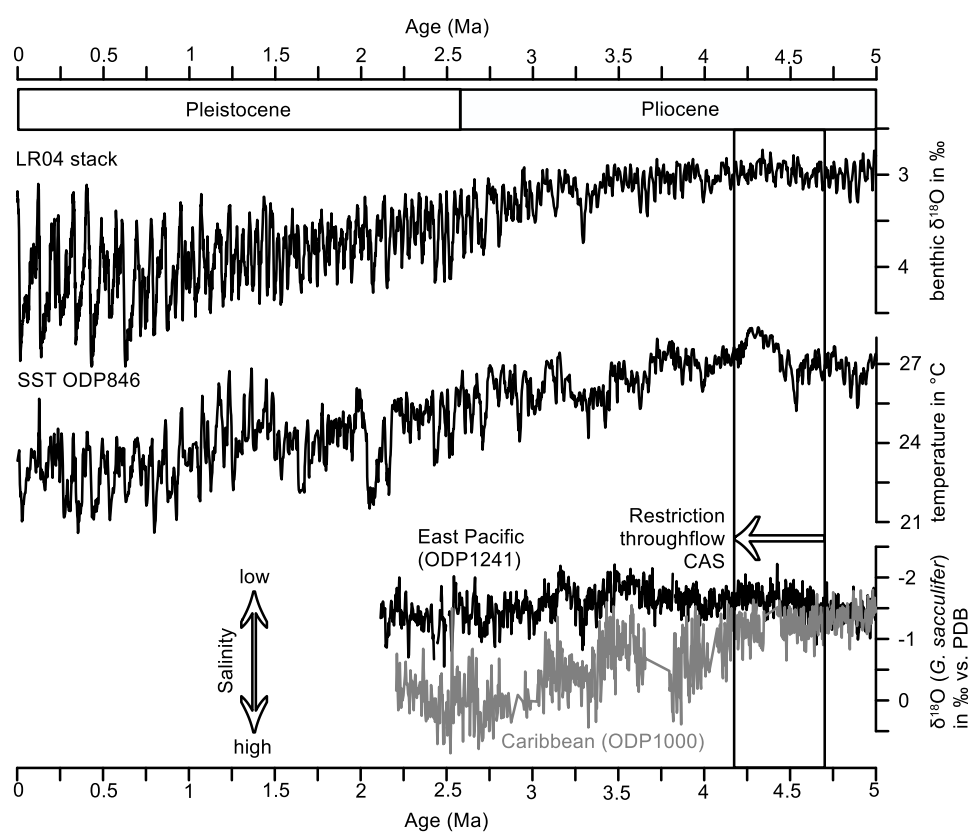
1 Introduction

The ~~progressive closure of the Central American Seaway (CAS) and the uplift of the northern Andes profoundly reorganized early Pliocene ocean and atmospheric circulation in the Eastern Equatorial Pacific (EEP). Pliocene epoch is characterized by some profound tectonic processes which altered oceanic and atmospheric circulation on a regional and possibly also global scale (Cannariato and Ravelo, 1997; Lunt et al., 2008). Two of these processes are the closure of the Isthmus of Panama and the uplift of the northern Andes.~~ The formation of the Isthmus of Panama, and especially the precise temporal constraints of the closure of the Panama Strait, have been subject of numerous studies (Bartoli et al., 2005; Groeneveld et al., 2014; Hoorn and Flantua, 2015; Montes et al., 2015; Steph, 2005). A recent review based on geological, paleontological, and molecular records narrowed the formation *sensu stricto* down to 2.8 Ma (O’Dea et al., 2016). Temporal constraints on the restriction of the surface water flow through the gateway were established by salinity reconstructions on both sides of the Isthmus (Steph et al., 2006b, Fig. 1). The salinities first start to diverge around 4.5 Ma. A major step in the seaway closure between 4.7 and 4.2 Ma was also assumed based on the comparison of mass accumulation rates of the carbonate sand-fraction in the Caribbean Sea and the EEP (Haug and Tiedemann, 1998). The closure of the Central American Seaway has been associated with the development of the EEP cold tongue (EEP CT), strengthened upwelling in the EEP, the shoaling of the thermocline, and a mean latitudinal shift of the [Intertropical Convergence Zone \(ITCZ\)](#); (Steph, 2005; Steph et al., 2006a; Steph et al., 2006b;

40 Steph et al., 2010). The direction of a potential shift of the ITCZ is still debated because of a discrepancy between paleoclimate
 41 reconstructions based on proxy data and numerical modelling results.

42 For the late Miocene, a northernmost paleoposition of the ITCZ at about 10–12°N has been proposed (Flohn, 1981; Hovan,
 43 1995). Subsequently, a southward shift towards 5°N paleolatitude between 5 and 4 Ma is indicated by eolian grain-size
 44 distributions in the eastern tropical Pacific (Hovan, 1995). Billups et al. (1999) provide additional evidence for a southward
 45 shift of the ITCZ between 4.4 and 4.3 Ma. Hence, most proxy data agree about a southward ITCZ shift during the early
 46 Pliocene. On the contrary, results from numerical modelling suggest a northward shift of the ITCZ in response to CAS closure
 47 (Steph et al., 2006b) and Andean uplift (Feng and Poulsen, 2014; Takahashi and Battisti, 2007).

48 An independent record of the terrestrial hydrology for the early Pliocene from a study site that is sensitive to latitudinal ITCZ
 49 shifts could provide new insights to this debate. Schneider et al. (2014) also stress the need of reconstructions of the ITCZ in
 50 the early and mid-Pliocene in order to understand how competing effects like an ice-free northern hemisphere and a weak EEP
 51 CT balanced, and to reduce uncertainties of predictions. Even though changes of ocean–atmosphere linkages related to ENSO
 52 (El Niño Southern Oscillation) and ITCZ shifts strongly impact continental precipitation in western equatorial South America,
 53 most studies so far have focused on paleoceanographic features such as sea–surface temperatures and ocean stratification.

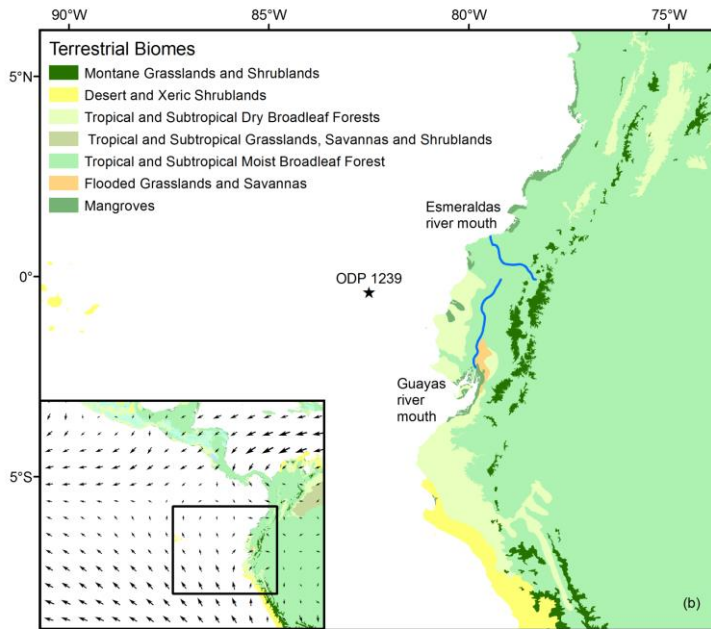
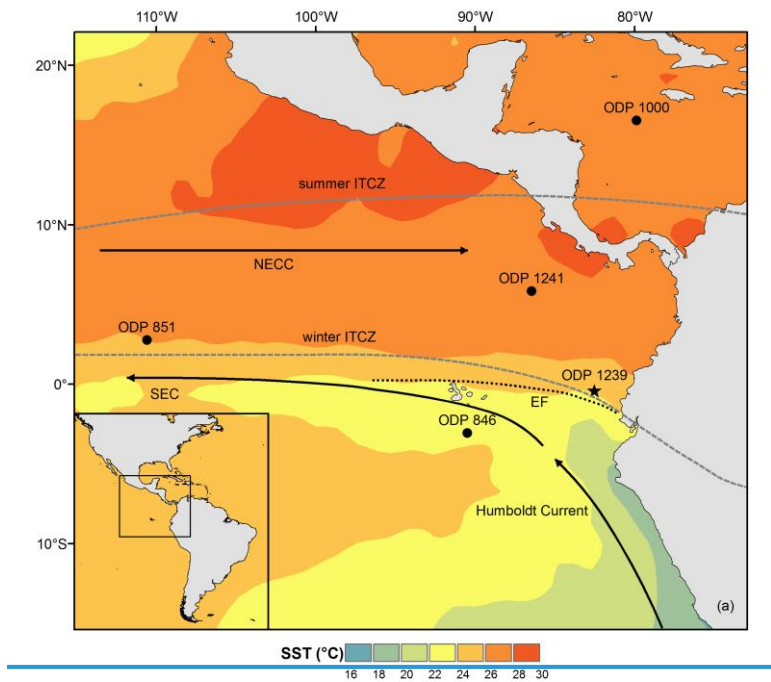


54
 55 **Figure 1:** LR04 global stack of benthic $\delta^{18}\text{O}$ reflecting changes in global ice volume and temperature (Lisiecki and Raymo, 2005).
 56 UK₃₇ sea–surface temperatures (SST) of ODP Site 846 in the Equatorial Pacific Cold Tongue (Lawrence et al., 2006). $\delta^{18}\text{O}$ of the
 57 planktonic foraminifer *G. sacculifer* from ODP Site 1000 in the Caribbean and ODP Site 1241 in the East Pacific (Haug et al., 2001;
 58 Steph, 2005; Steph et al., 2006a), reflecting changes in sea–surface salinity (see Fig. 2 for location of ODP Sites). The box represents
 59 the time window analyzed in this study.

60
 61 The second major tectonic process is the uplift of the Northern Andes which strongly altered atmospheric circulation patterns
 62 over South America. Three major deformation phases include fan building in the lower Eocene to early Oligocene,
 63 compression of Oligocene deposits in the Miocene and Pliocene, and refolding during Pliocene to recent times (Corredor,
 64 2003). While the uplift of the Central Andes is well investigated, only few studies deal with the timing of uplift of the Northern
 65 Andes. Coltorti and Ollier (2000), based on geomorphologic data, conclude that the uplift of the Ecuadorian Andes started in
 66 the early Pliocene and continued until the Pleistocene. More recent apatite fission track data indicate that the western Andean

67 Cordillera of Ecuador was rapidly exhumed during the late Miocene (13–9 Ma) (Spikings et al., 2005). Uplift estimates for the
68 Central Andes suggest that the Altiplano had reached less than half of its modern elevation by 10 Ma, with uplift rates
69 increasing from 0.1 mm/yr in the early and middle Miocene to 0.2–0.3 mm/yr to present. For the Eastern Cordillera of
70 Colombia, elevations of less than 40% of the modern values are estimated for the early Pliocene, then increasing rapidly at
71 rates of 0.5–3 mm/yr until modern elevations were reached around 2.7 Ma (Gregory-Wodzicki, 2000). Both the tectonic events
72 and the closure of the Central American Seaway are assumed to have had a large impact on ocean and atmospheric circulation
73 in the eastern Pacific, the Caribbean and on adjacent land masses. Therefore, the reconstruction of continental climate,
74 especially hydrology, will contribute to our understanding of climatic changes in this highly complex area.

75 To better understand the early Pliocene vegetation and hydrology of western equatorial South America we studied pollen and
76 spores from the early Pliocene section (4.7–4.2 Ma) of the marine sediment record at ODP Site 1239 and compared this record
77 to Holocene samples from the same Site. [In addition, we use elemental ratios to estimate variations in fluvial terrestrial input](#)
78 [\(Ríncon-Martínez et al. 2010\)](#). While other palynological studies of the region have been conducted for the mid-Pliocene to
79 Holocene (González et al., 2006; Hooghiemstra, 1984; Seilles et al., 2016), [only a few palynological records for the early](#)
80 [Pliocene exist \(Wijninga and Kuhry, 1990; Wijninga, 1996\)](#). ~~this is the first palynological record of western equatorial South~~
81 ~~America from the early Pliocene~~. The record contributes to elucidate how vegetation and climate in this area responded to
82 changes in atmospheric and oceanic circulation, possibly induced by the closure of the Central American Seaway and the uplift
83 of the northern Andes. Therefore the main objectives of the study are firstly, to investigate long-term vegetation and climatic
84 changes, focusing on hydrology, in western equatorial South America and, secondly, to interpret these changes in relation to
85 climate phenomena influencing the hydrology of the region, especially the mean latitudinal position of the ITCZ and variability
86 related to ENSO. These objectives are approached by the following research questions: 1) What floral and vegetation changes
87 took place in the coastal plain ~~and the Western Andean Cordillera~~ of western equatorial South America [and the Ecuadorian](#)
88 [Andes](#) from 4.7 to 4.2 Ma? 2) What are the climatic implications of the vegetation change, especially in terms of hydrology?
89 3) What are the implications for Andean uplift, especially regarding the development of the high Andean páramo vegetation?



90

91

92

93

94

95

96

97

98

99

100

101

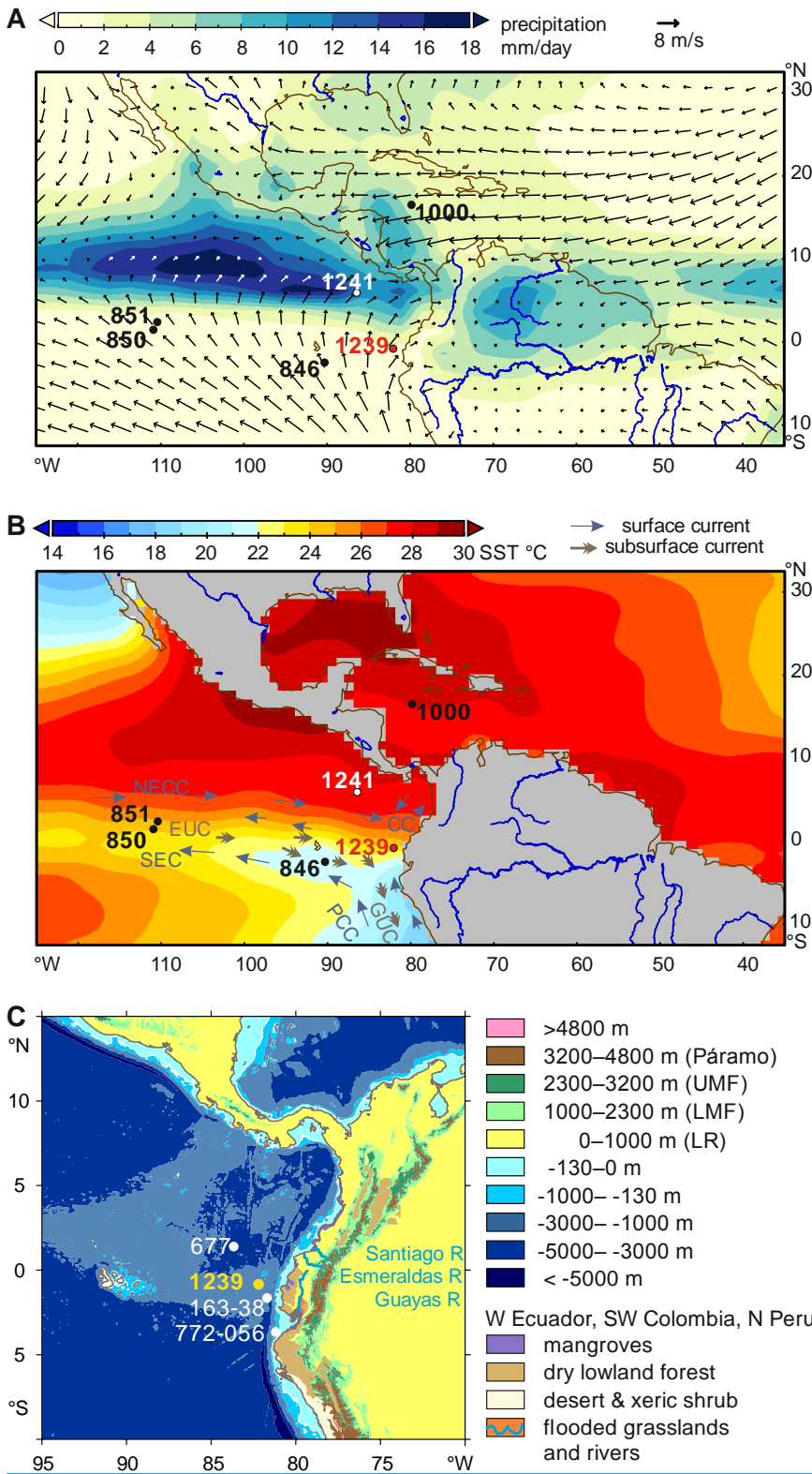
102

103

104

105

Figure 2. Modern climate (boreal summer) and vegetation and core site positions of ODP Sites 677, 846, 850, 851, 1000, 1239, 1241, Trident core TR163-38, and M772-056 mentioned in the text. A. Long term monthly July precipitation in mm/day (CPC) and wind field (NCEP). July is the middle of the rainy season in northern South America, when the ITCZ is at its northern boreal summer position. Salinity estimates for the Caribbean indicate a position of the ITCZ further north during the Pliocene. Direction of wind is not favorable for wind transport of pollen and spores to ODP Site 1239. B. Long term monthly July sea surface temperatures (NODC), surface and subsurface currents of the eastern equatorial Pacific (Mix et al. 2003). NECC, North Equatorial Countercurrent; SEC, South Equatorial Current; PCC, Peru-Chile Current (continuation of the Humboldt Current); CC, Coastal Current; EUC, Equatorial Undercurrent; GUC, Gunther Undercurrent. C. Contours, bathymetry (ETOPO1), main rivers in Ecuador, and vegetation. Transport of pollen and spores in the ocean over the Peru-Chile Trench, which is very narrow east of the Carnegie Ridge, probably takes place in nepheloid layers. Páramo vegetation is found between 3200 and 4800 m, upper montane Andean forest (UMF) grows between 1000 and 2300 m, sub-Andean lower montane forest (LMF) between 1000 and 2300 m, and lowland forest (LR) below 1000m. The distribution of desert and xeric shrubs in northern Peru, drier broad leaved forest, flooded grasslands, and mangroves in Ecuador and Colombia is denoted in different colors (see legend, WWF). Source areas of pollen and spores in sediments of ODP Site 1239 are sought in western Ecuador, northwestern Peru, and southwestern Colombia (see text). Abbreviated web sources and retrieval dates are listed under references.



106

107 **Figure 2:** (a) Major oceanographic features of the eastern equatorial Pacific (SST: Sea surface temperature, statistical annual mean
 108 from 2005–2012 from NOAA; NECC: North Equatorial Counter Current, SEC: South Equatorial Current, EF: Equatorial Front),
 109 and boreal summer and winter position of the Intertropical Convergence Zone (ITCZ). The locations of ODP Sites mentioned in the
 110 text are indicated. (b) Modern vegetation of western equatorial South America as defined by the World Wildlife Fund (please note
 111 that the terrestrial biomes are not identical to the altitudinal vegetation belts shown in Fig. 3 and 4), major rivers draining into the
 112 Pacific, and magnitude and direction of January surface winds (NCEP Reanalysis Derived monthly long-term means from 1981–
 113 2010 provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website at <http://www.esrl.noaa.gov/psd/>).
 114 **Figure 2. Modern climate (boreal summer) and vegetation and core site positions of ODP Sites 677, 846, 850, 851, 1000, 1239, 1241,**
 115 **Trident core TR163-38, and M772-056 mentioned in the text. A. Long-term monthly July precipitation in mm/day (CPC) and wind**
 116 **field (NCEP). July is the middle of the rainy season in northern South America, when the ITCZ is at its northern boreal summer**
 117 **position. Salinity estimates for the Caribbean indicate a position of the ITCZ further north during the Pliocene. Direction of wind is**
 118 **not favorable for wind transport of pollen and spores to ODP Site 1239. B. Long-term monthly July sea-surface temperatures**
 119 **(NODC), surface and subsurface currents of the eastern equatorial Pacific (Mix et al. 2003). NECC, North Equatorial**
 120 **Countercurrent; SEC, South Equatorial Current; PCC, Peru-Chile Current (continuation of the Humboldt Current); CC, Coastal**

121 Current; EUC, Equatorial Undercurrent; GUC, Gunther Undercurrent. C. Contours, bathymetry (ETOPO1), main rivers in
122 Ecuador, and vegetation. Transport of pollen and spores in the ocean over the Peru-Chile Trench, which is very narrow east of the
123 Carnegie Ridge, probably takes place in nepheloid layers. Páramo vegetation is found between 3200 and 4800 m, upper montane
124 Andean forest (UMF) grows between 1000 and 2300 m, sub-Andean lower montane forest (LMF) between 1000 and 2300 m, and
125 lowland forest (LR) below 1000m. The distribution of desert and xeric shrubs in northern Peru, drier broad-leaved forest, flooded
126 grasslands, and mangroves in Ecuador and Colombia is denoted in different colors (see legend, WWF). Source areas of pollen and
127 spores in sediments of ODP Site 1239 are sought in western Ecuador, northwestern Peru, and southwestern Colombia (see text).
128 Abbreviated web sources and retrieval dates are listed under references.

1.1 Modern setting

1.1.1 Climate and ocean circulation

132 The climate of western equatorial South America is complex and heterogeneous, as it is not only controlled by large-scale
133 tropical climate phenomena such as the ITCZ and ~~the El Niño Southern Oscillation (ENSO)~~, but is also strongly influenced by
134 small-scale climate patterns caused by the diverse Andean topography (Marchant et al., 2001; Niemann et al., 2010). The
135 annual cycle of precipitation in northwestern South America is controlled by insolation changes. During boreal summer when
136 insolation is strongest in the northern hemisphere, the ITCZ is located at its northernmost position around 9°–10° N (Vuille et
137 al., 2000). Approaching austral summer, the ITCZ moves southward across the equator. Within the range of the ITCZ, annual
138 precipitation patterns are generally characterized by two minima and two maxima. The coastal areas of southern Ecuador
139 where the ITCZ has its southernmost excursion show an annual precipitation pattern with one maximum during austral summer
140 and a pronounced dry season during austral winter (Bendix and Lauer, 1992).

141 This general circulation pattern is modified by ENSO at interannual time-scales. During warm El Niño events, the lowlands
142 of Ecuador experience abundant precipitation whereas the northwestern Ecuadorian Andes experience drought (Vuille et al.,
143 2000). Regional climate patterns are also modified by the topography of the Andes which pose an effective barrier for the
144 large-scale atmospheric circulation. While precipitation patterns east of the Andes are driven by moisture-laden easterly trade
145 winds originating over the tropical Atlantic and the Amazon basin, the coastal areas and the western Andean slopes are
146 dominated by air masses originating in the Pacific (Vuille et al., 2000, Fig. 2). The warm annual El Niño current which flows
147 southward along the Colombian Pacific coast warms the air masses along the coast. This moist air brings over 6000 mm yearly
148 precipitation to the northern coastal plain (Balslev, 1988). In contrast, the coastal areas of southernmost Ecuador and northern
149 Peru are under the influence of the Peru-Chile Current, which is a continuation of the cold Humboldt Current ~~which~~
150 transporting cold and nutrient rich waters and giving rise to a long strip of coastal desert. The westwards flow of the cold
151 surface waters of the EEP CT to the western Pacific via the South Equatorial Current (SEC) is driven by the Walker Circulation.
152 Warm waters return eastwards via the North Equatorial Countercurrent (NECC, see Fig. 2). An abrupt transition between the
153 cold SEC and the warm NECC is the Equatorial Front (EF).

1.1.2 Geography, vegetation and pollen transport

155 The study areaEcuador is geographically divided into three main regions: the coastal plain with several rivers draining into the
156 Pacific, the Andes, and the eastern lowlands which constitute the western margin of the Amazon Basin. The mountains form
157 two parallel cordilleras which are separated by the Interandean Valley. The diverse vegetation is the result of the combined
158 effects of elevation and precipitation. In the coastal plain there is an abrupt shift from tropical lowland rainforests in the north
159 to a desert dominated by annual xerophytic herbs in the south. This shift reflects the dependence of the vegetation on
160 precipitation which ranges from 100 to 6000 mm per year on the coastal plain. The western slopes of the Andes are covered
161 by montane forest, which is partly interrupted by drier valleys in southern Ecuador (Balslev, 1988).

162 Along the coast, mangrove stands occur in the salt- and brackish-water tidal zone of river estuaries and bays. They are formed
163 by two species of *Rhizophora* (*R. harrisonii* and *R. mangle*), and to a lesser extent *Avicennia*, *Laguncularia*, and *Conocarpus*
164 are present (Twilley et al., 2001). The lowland rainforest is characterized by the dominant plant families Fabaceae, Rubiaceae,

165 ~~Palmae~~Arecaceae, Annonaceae, Melastomataceae, Sapotaceae, and Clusiaceae in terms of species richness. In the understory,
166 Rubiaceae, Araceae, and Piperaceae form the predominant elements (Gentry, 1986). In the lower montane forest, *Cyathea*,
167 Meliaceae (e.g. *Ruagea*), Fabaceae (e.g. *Dussia*), Melastomataceae (e.g. *Meriania*, *Phainantha*), Rubiaceae (e.g. *Cinchona*),
168 Proteaceae (e.g. *Roupala*), Lauraceae (e.g. *Nectandra*), and Pteridaceae (e.g. *Pterozonium*) are common elements. Upper
169 montane forests are dominated by *Myrsine*, *Ilex*, *Weinmannia*, *Clusia*, *Schefflera*, *Myrcianthes*, *Hedyosmum*, and *Oreopanax*
170 (Jørgensen et al., 1999).

171 Above ca. 3200 m, trees become sparse and eventually the vegetation turns into páramo. The páramo is a unique ecosystem of
172 the high altitudes of the northern Andes of South America and of southern Central America, located between the continuous
173 forest line and the permanent snowline at about 3000–5000 m (Luteyn, 1999). The grass páramo is formed by tussock grasses,
174 mainly *Calamagrostis* and *Festuca*. These are complemented by shrubs of *Diplostephium*, *Hypericum*, and *Pentacalia*, and
175 forest patches of *Polylepis*. The shrub páramo consists of cushion plants like *Azorella*, *Plantago*, and *Werneria*, and shrubs
176 like *Loricaria* and *Chuquiraga*. The vegetation of the desert páramo is scarce. Some common taxa are *Nototriche*, *Draba*, and
177 *Culcitium* (Sklenar and Jorgensen, 1999).

178 ~~Rincon-Martínez et al. (2010) showed that the terrigenous sediment supply at ODP Site 1239 during Pleistocene interglacials~~
179 ~~is mainly fluvial and input of terrestrial material drops to low amounts during the drier glacial stages. Consequently, transport~~
180 ~~of pollen and spores to the ocean is also mainly fluvial (González et al., 2010). High rates of orographic precipitation~~
181 ~~characterize the western part of equatorial South America. These heavy rains quickly wash out any pollen that might be in the~~
182 ~~air and result in large discharge by the Ecuadorian Rivers (Fig. 2). Esmeraldas and Santiago Rivers mainly drain the northern~~
183 ~~coastal plain of Ecuador, and the southern coastal plain is drained by several smaller rivers, which end in the Guayas River.~~
184 ~~Moreover, the predominantly westerly winds (Fig. 2) are not favorable for eolian pollen dispersal to the ocean. Nevertheless,~~
185 ~~some transport by SE trade winds is possible and should be taken into account.~~

186 ~~After reaching the ocean, pollen and spores might pass the Peru-Chile Trench – which is quite narrow along the Carnegie~~
187 ~~Ridge – by means of nepheloid layers at subsurface depths. Some northward transport from the Bay of Guayaquil by the~~
188 ~~Coastal Current (Fig. 2) is likely. However, the Peru-Chile Current flows too far from the coast to have strong influence on~~
189 ~~pollen and spore dispersal. We consider western Ecuador, northernmost Peru and southwestern Colombia the main source~~
190 ~~areas of pollen and spores in sediments of ODP Site 1239. The high rates of orographic precipitation that characterize the~~
191 ~~western part of equatorial South America cause pollen grains to be washed down by the rain quickly. Therefore, the main~~
192 ~~transport agent are the rivers draining into the Pacific. The northern coastal plain of Ecuador is mainly drained by the~~
193 ~~Esmeraldas and Santiago Rivers, and the southern coastal plain is drained by several smaller rivers which end in the Guayas~~
194 ~~River. From the river mouths, pollen might cross the Peru-Chile Trench in nepheloid layers to reach the Carnegie Ridge.~~

195 1.1.3 Drilling site

196 ODP Site 1239 is located at 0°40.32'S, 82°4.86'W, about 120 km offshore Ecuador in a water depth of 1414m, near the eastern
197 crest of Carnegie Ridge and just next to a downward slope into the Peru-Chile Trench (Mix et al., 2003). Its location is close
198 to the Equatorial Front (Fig. 2) which separates the warm and low-salinity waters of Panama Basin from the cooler and high-
199 salinity surface waters of the EEP CT. The region of Site 1239 reveals a thick sediment cover, with dominant sediments in the
200 region being foraminifer-bearing diatom nannofossil ooze. A tectonic backtrack path on the Nazca plate (Pisias, 1995) reveals
201 a paleoposition of Site 1239 about 150–200 km further westward (away from the continent) and slightly southward relative to
202 South America at 4–5 Ma compared to the present day position (Mix et al., 2003). The sediments of Carnegie Ridge are
203 characterized by high smectite values. Due to its proximity to the Ecuadorian coast, Site 1239 is suitable to record changes in
204 fluvial runoff, related to variations of precipitation in northwestern South America. Most of the material is discharged by the
205 Guayas River and Esmeraldas River (Rincon-Martinez et al., 2010).

207
208
209
210
211

Table 1.: List of identified pollen and spore taxa in marine ODP Holes 1239A (Pliocene samples) and 1239B (core top samples, taxa in grey occurred only in core top samples) and grouping according to their main ecological affinity (Flantua et al., 2014; Marchant et al., 2002).

<u>Páramo</u>	<u>Upper montane forest</u>	<u>Lower montane forest</u>	<u>Lowland rainforest</u>	<u>Broad range taxa</u>	<u>Humid indicators</u>
<i>Polylepis/Acaena</i>	<u>Podocarpaceae</u>	<u>Urticaceae/Moraceae</u>	<u>Wettinia</u>	<u>Poaceae</u>	<u>Cyperaceae</u>
<i>Jamesonia/Eriosorus</i>	<u>Hedyosmum</u>	<u>Erythrina</u>	<u>Socratea</u>	<u>Cyperaceae</u>	<u>Ranunculus</u>
<i>Huperzia</i>	<u>Clethra</u>	<u>Alchornea</u>	<u>Polypodiaceae</u>	<u>Tubuliflorae (Asteraceae)</u>	<u>Hedyosmum</u>
<i>Ranunculus</i>	<u>Morella</u>	<u>Styloceras T</u>	<u>Pityrogramma/Pteris altissima T</u>	<u>Amaranthaceae</u>	<u>Ilex</u>
<i>Draba</i>	<u>Acanthaceae</u>	<u>Malpighiaceae</u>		<u>Rosaceae</u>	<u>Pachira</u>
<i>Sisyrinchium</i>	<u>Melastomataceae</u>	<u>Cyatheaceae</u>		<u>Ambrosia/Xanthium</u>	<u>Morella</u>
<i>Cystopteris diaphana T</i>	<u>Daphnopsis</u>	<u>Vernonia T</u>		<u>Ericaceae</u>	<u>Malpighiaceae</u>
	<u>Bocconia</u>	<u>Pteris grandifolia T</u>		<u>Artemisia</u>	<u>Cyatheaceae</u>
	<u>Myrsine</u>	<u>Pteris podophylla T</u>		<u>Ilex</u>	<u>Selaginella</u>
	<u>Lophosoria</u>	<u>Saccoloma elegans T</u>		<u>Thevetia</u>	<u>Pityrogramma/Pteris altissima T</u>
	<u>Elaphoglossum</u>	<u>Thelypteris</u>		<u>Salacia</u>	<u>Hymenophyllum T</u>
	<u>Hypolepis hostilis T</u>	<u>Ctenitis subincisa T</u>		<u>Bromeliaceae</u>	<u>Thelypteris</u>
	<u>Grammitis</u>			<u>Malvaceae</u>	<u>Ctenitis subincisa T</u>
	<u>Dodonaea viscosa</u>			<u>Euphorbiaceae</u>	<u>Alnus</u>
	<u>Alnus</u>			<u>Liliaceae</u>	<u>Cystopteris diaphana T</u>
				<u>Lycopodiaceae excl. Huperzia</u>	
				<u>Selaginella</u>	
				<u>Hymenophyllum T</u>	
				<u>Calandrinia</u>	

212
213

214 2 Methods

215 A total of 65 samples of 10 cm³ volume have been analyzed. For the interval between 301 and 334 m (4.7 and 4.2 Ma), 46
 216 sediment samples of 10 cm³ volume were taken at 67 cm intervals on average from ODP Hole 1239A (cores 33X5-37X1).
 217 Seventeen samples were taken more or less regularly distributed over the rest of the upper 450 m of Hole A (until 6 Ma).
 218 Additionally, two core top samples were taken from ODP Hole 1239B as modern analogues. Standard analytical methods were
 219 used to process the samples, including decalcification with HCl (~10%) and removal of silicates with HF (~40%). Two tablets
 220 of exotic *Lycopodium* spores (batch #177,745 containing 18584 ± 829 spores per tablet) were added to the samples during the
 221 decalcification step for calculation of pollen concentrations (grains/cm³). After neutralization with KOH (40%) and washing,
 222 the samples were sieved with ultrasound over an 8µm screen to remove smaller particles. Samples were mounted in glycerin

and a minimum of 100 pollen/spore grains (178 on average, [Supplementary Figure](#)) were counted in each sample using a Zeiss Axioskop and 400x and 1000x (oil immersion) magnification.

For pollen identification, the Neotropical Pollen Database (Bush and Weng, 2007), a reference collection for Neotropical species held at the Department of Palynology and Climate Dynamics in Göttingen, and related literature (Colinvaux et al., 1999; Hooghiemstra, 1984; Murillo and Bless, 1974, 1978; Roubik and Moreno, 1991) were used. Pollen types were grouped according to their main ecological affinity (Flantua et al., 2014; Marchant et al., 2002). The zonation of the diagrams was based on constrained cluster analysis by sum-of-squares (CONISS) [of the pollen percentage curves](#), using the square root transformation method (Edwards & Cavalli-Sforza's chord distance) implemented in TILIA (Grimm, 1991, [Supplementary Figure](#)) [and visual inspection of the pollen percentage curves](#) ([Supplementary Figure](#)). Percentages are based on the pollen sum, which includes all pollen and fern spore types including unidentifiable ones. Confidence intervals were calculated after Maher (1972). An initial age model for Site 1239 was established based on biostratigraphic information (Mix et al., 2003). The age model was refined by matching the benthic stable isotope records from Site 1239 with those from Site 1241 by visual identification of isotope stages. 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). A [hiatus-coring gap](#) of ca. 5 meters exists between cores 35X and 36X of Hole 1239A (Tiedemann et al., 2007; [Table AT3](#)).

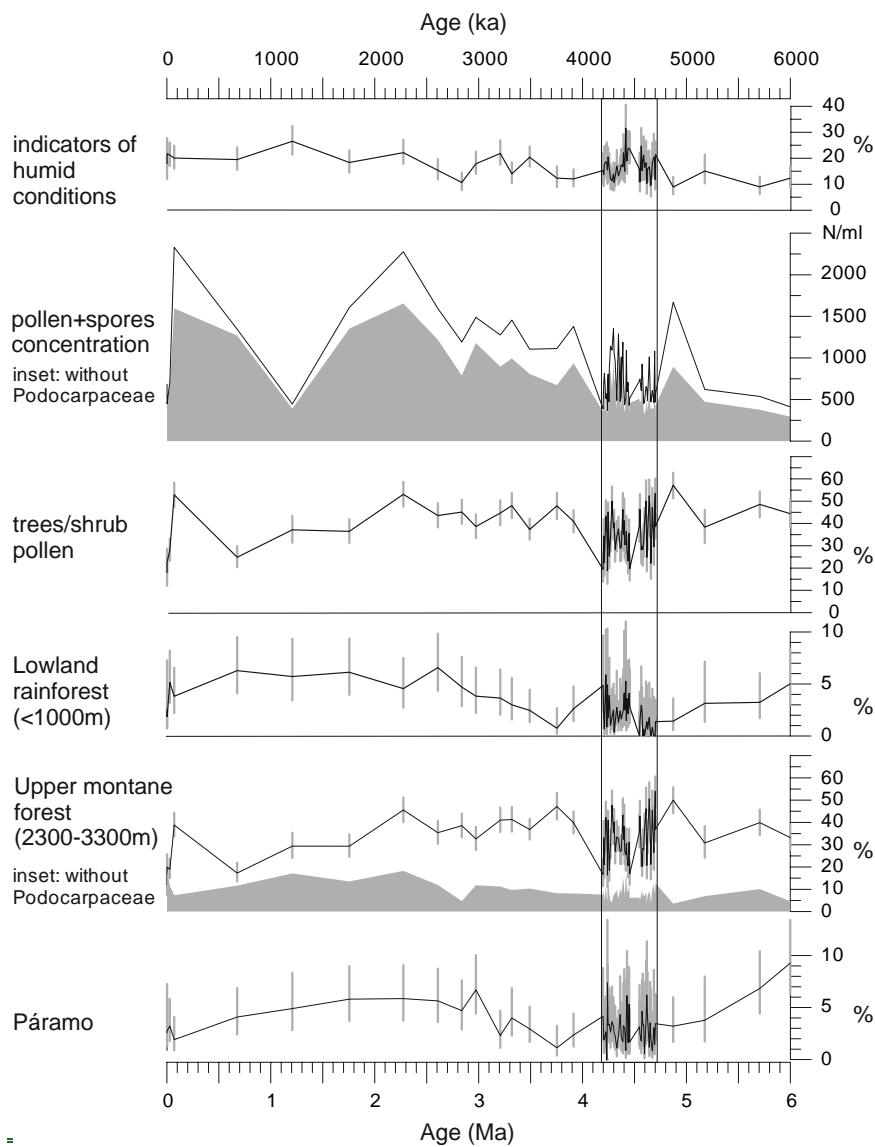
Elemental concentrations (total elemental counts) of Fe and K were measured in high resolution (every 2 cm) using an Avaatech™ X-Ray Fluorescence (XRF) Core Scanner at the Alfred-Wegener-Institute, Bremerhaven. Both Holes A and B of ODP Site 1239 were sampled. A nondestructive measuring technique was applied, allowing rapid semi-quantitative geochemical analysis of sediment cores (Richter et al., 2006). Several studies comparing XRF core scanner data to geochemical measurements on discrete samples showed that major elements such as Fe, Ca, and K can be precisely measured with the scanner in a non-destructive way (e.g. Tjallingii et al., 2007).

3 Results

Five groups were established with pollen taxa grouped according to their main ecological affinity (Table 1). The groups páramo, upper montane forest, lower montane forest, and lowland rainforest represent vegetation belts with different altitudinal ranges (Hooghiemstra, 1984; Van der Hammen, 1974). To track changes of humidity, an additional group named “Indicators of humid conditions” was established. This group includes those taxa [which that](#) permanently need humid conditions to grow. Changes of the pollen percentages of the ecological groups for the Pliocene interval and the core top samples are shown in [Figs. 3 and 35](#). Pollen percentages of single taxa are shown in [the supplementary Supplementary Figure-S1](#). [Taxa that occurred in less than 10% of the samples were excluded from the interpretation.](#)

[To put the results of the detailed early Pliocene section into context of long-term changes, we plot a selection together with the results of a coarse resolution pilot study in Fig. 3. Percentages of humidity indicators hint to slightly drier conditions at the beginning of the Pliocene. A trend towards higher palynomorph concentrations is found for the period from 6 to 2 Ma. Grass pollen percentages remain low indicating mainly closed forest at altitudes below the páramo. Representation of lowland rainforest was low around 4.7 Ma, increased by 4.5 Ma, declined again to low levels around 3.5 Ma, and rose to remain at higher levels during the Pleistocene. Continuous presence of pollen and spores from the páramo indicates that the Ecuadorian northern Andes had reached high altitudes in Ecuador before the Pliocene.](#)

[Figure 3. Pliocene and Pleistocene palynomorph percentages \(based on the total of pollen and spores\) of ODP Hole 1239A for three vegetation belts, humidity indicators, grass pollen and pollen and spore concentration per ml. 95% confidence intervals as grey bars after Maher \(1972\). Age model for the last 5 Ma after Tiedemann et al. \(2007\) and for 6 to 5 Ma after Mix et al. \(2003\).](#)



263

264

265

266

Figure 3. Pliocene and Pleistocene palynomorph percentages (based on the total of pollen and spores) of ODP Hole 1239A for three vegetation belts, humidity indicators, grass pollen and pollen and spore concentration per ml. 95% confidence intervals as grey bars after Maher (1972). Age model for the last 5 Ma after Tiedemann et al. (2007) and for 6 to 5 Ma after Mix et al. (2003).

267

3.1 Modern vs. Pliocene pollen assemblages

268

269

270

271

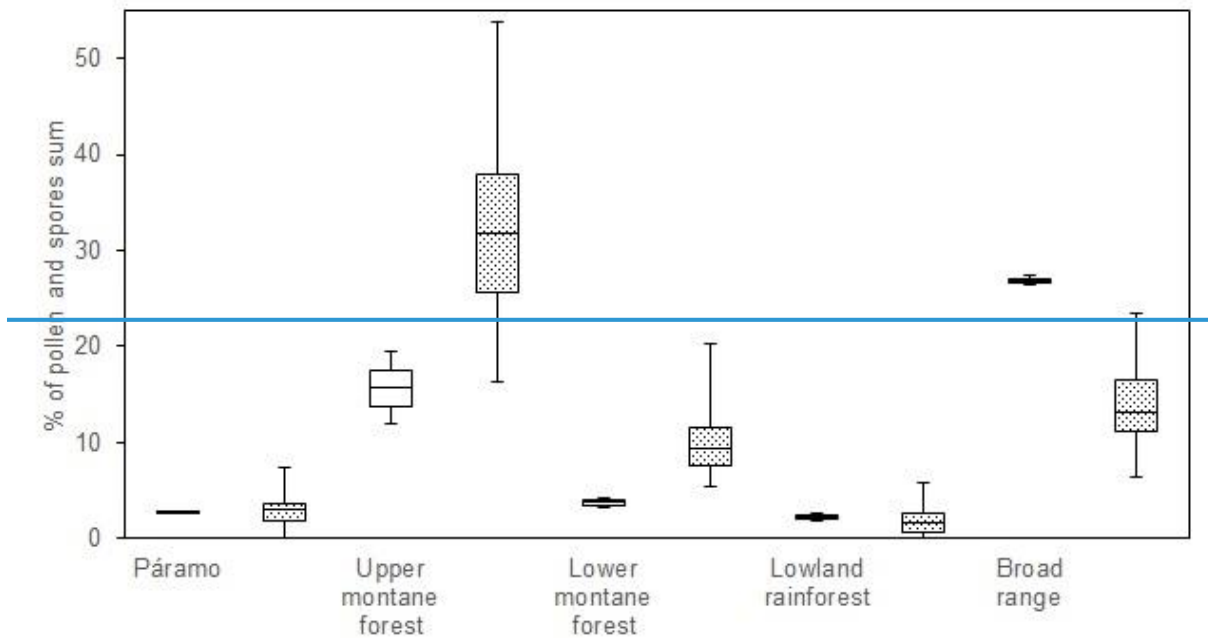
272

273

274

275

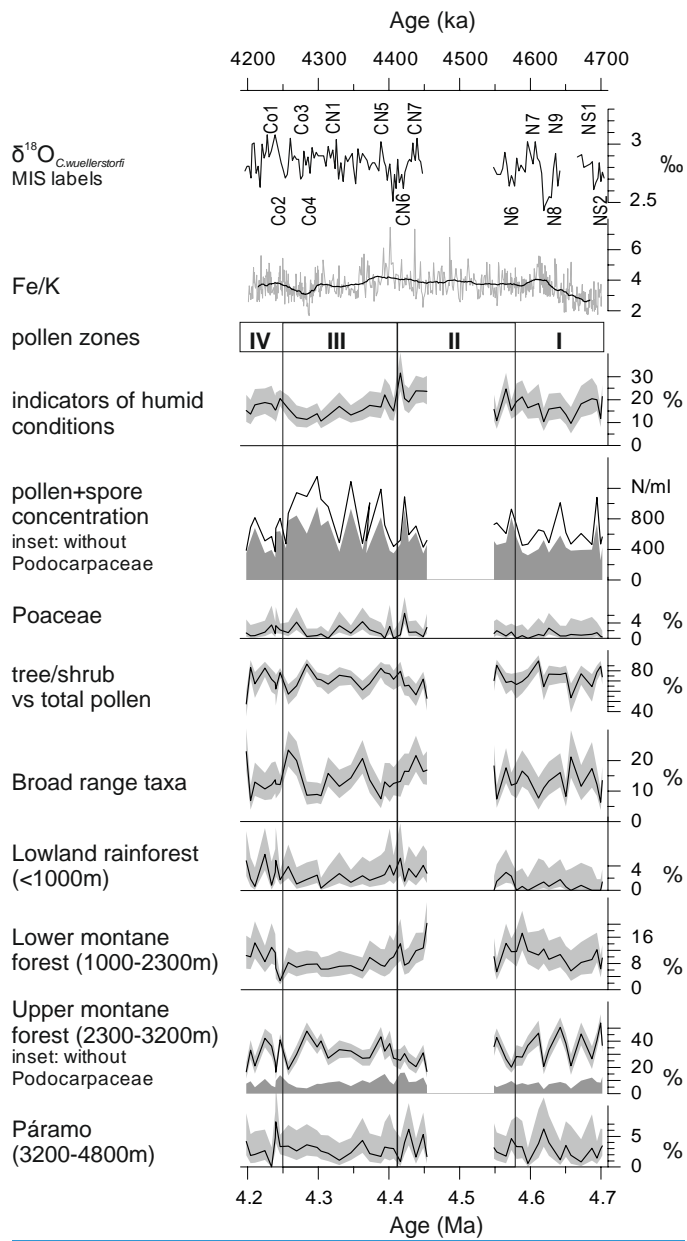
Fifty one different palynomorph types were recognized, including 29 pollen and 22 fern spore types. The samples are characterized by low pollen and spore concentrations of 685 and 465 grains/cm³, respectively. Indicators of humid conditions show intermediate values. Herbs and grass pollen are very abundant with 20–26%, but tree and shrub pollen decreased to 35–46% compared to the Pliocene interval. Broad range taxa reach their maximum abundance with 26–27%. Lowland rainforest and páramo pollen have similar representations as in the Pliocene, whereas the lower and upper montane forest pollen reach their lowest percentages. When compared to the Pliocene pollen composition, some floristic differences are seen, whereof the most prominent is the replacement of Podocarpaceae as the most abundant upper montane forest trees by *Alnus*. Another notable difference is the presence of *Rhizophora* pollen in one of the core top samples, whereas it is completely absent in the Pliocene interval.

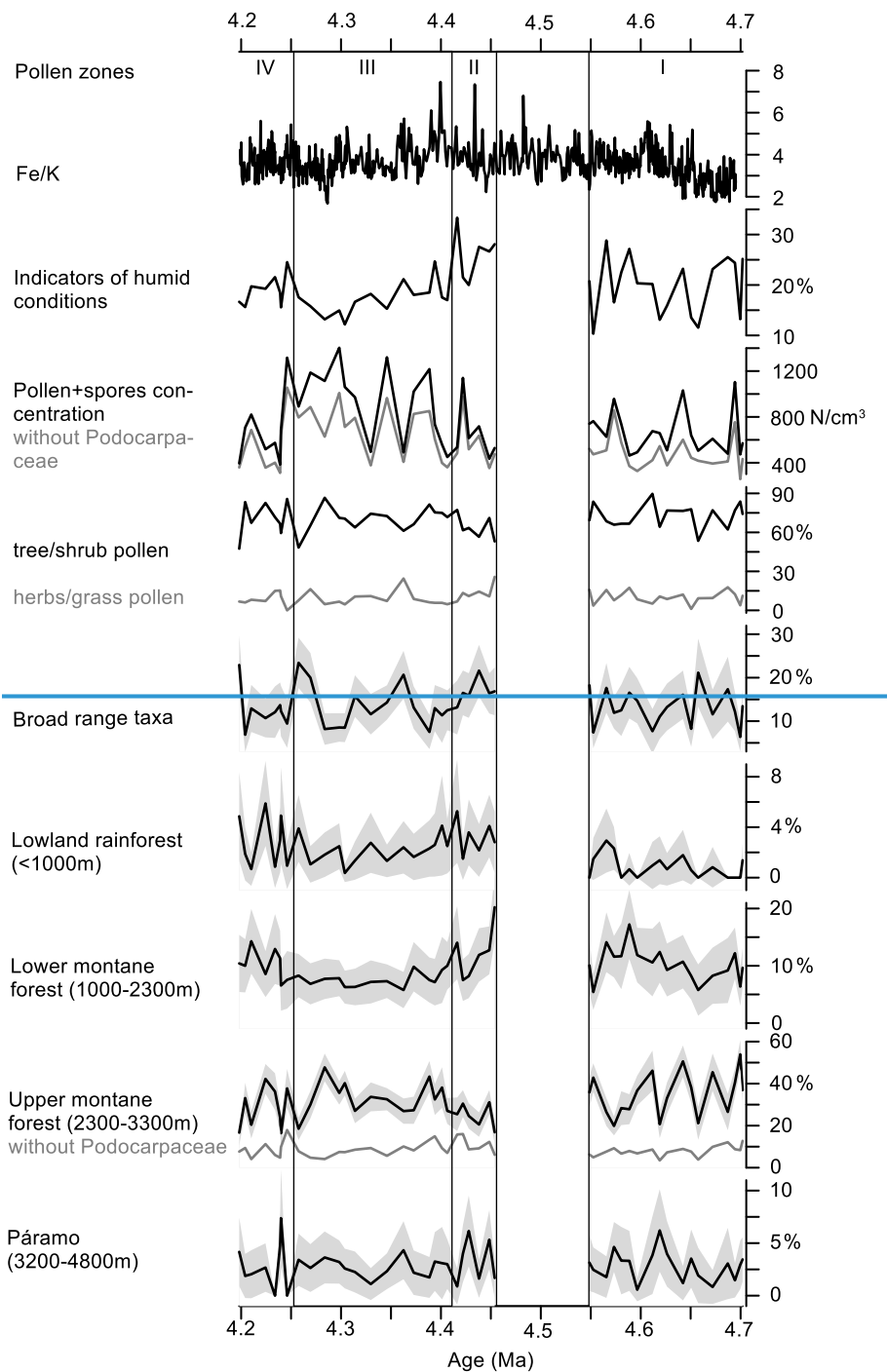


276
277 **Figure 3: Comparison of the relative percentages of the different vegetation belts between core top samples (left, plain) and Pliocene**
278 **samples (right, dotted).**

279 **3.2.1 Description of the early Pliocene pollen record**

280 In the early Pliocene samples, 141 different palynomorph types were recognized, including 77 pollen and 64 fern spore types.
281 A high percentage of tree and shrub pollen (46–88%) is present throughout the interval, compared to a low percentages of
282 herbs and grass pollen (0–25%; Fig. 4). In most of the vegetation belts, one or two pollen or spore taxa are overrepresented.
283 The lowland rainforest is mainly represented by Polypodiaceae, the lower montane forest is controlled by Cyatheaceae, and
284 the upper montane forest is strongly influenced by Podocarpaceae and *Hedyosmum*. In the páramo, the percentages of the
285 pollen taxa are more evenly balanced. Of the total sum, the Andean forest pollen makes by far the largest percentage, with the
286 upper montane forest ranging between 17 and 54% and the lower montane forest between 5 and 19%. The páramo is
287 represented with 0 to 10% and the lowland rainforest with 0 to 6%. The remaining fraction has a wide or unknown ecological
288 range.
289





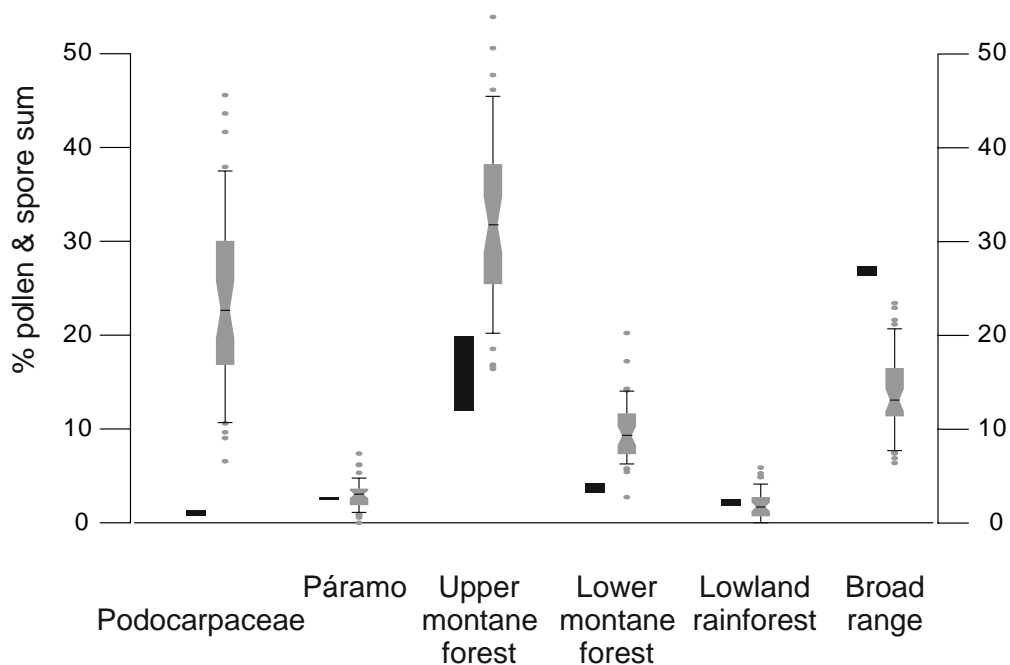
291

292 **Figure 4.3:** Palynomorph percentages of ODP Hole 1239A for the four vegetation belts and other groups from 4.7 to 4.2 Ma. Grey
 293 shading represents the 95% confidence intervals (after Maher, 1972). Vertical black lines delimit the pollen zones. At the top stable
 294 oxygen isotopes of the benthic foraminifer *C. wuellerstorfi* (Tiedemann et al., 2007) of ODP Hole 1239A, marine isotope stages (MIS),
 295 and ~~On-top~~ elemental ratios of Fe/K from Holes 1239A and 1239B. Ages are from Tiedemann et al. (2007). A coring gap hiatus is
 296 present in Hole 1239A between 4.45 and 4.55 Ma.

297

298 The pollen record of ODP Hole 1239A was divided into four main pollen zones based on constrained cluster analysis (Fig. 4
 299 and Supplementary Figure). Pollen zone I (333.4–325.2 mbsf: 4.70–4.55–58 Ma, 18–14 samples) has low pollen and spores
 300 concentrations. It is characterized by low pollen percentages of lowland rainforest, increases in pollen values of lowland
 301 rainforest, lower montane forest, the percentage of fern spores, and the Fe/K ratio. The pollen concentrations of broad range
 302 taxa, upper montane forest, páramo, and indicators of humid conditions go through frequent fluctuations. Coastal desert herbs
 303 (Amaranthaceae) are well represented (Supplementary Figure). Percentages of Poaceae pollen are low. Between pollen zone I
 304 and II, a hiatus of about 51.7 ka is present. In pollen zone II (319.324.84–316.4 mbsf: 4.456–4.42 Ma, 106 samples), the pollen

305 and spores concentration is similar to pollen zone I. The lowland rainforest pollen, indicators of humid conditions, and the
 306 Fe/K ratio reach their maximum. Fern spores also reach their first maximum. Percentages of lower montane forest and páramo
 307 are high, whereas the percentage of upper montane forest is low at this time due to a strong decline of Podocarpaceae pollen.
 308 The representation of broad range taxa diminish in this interval above the gap, the decrease being mainly controlled by
 309 *Selaginella*, Cyperaceae, *Ambrosia/Xanthium*, and Amaranthaceae. Pollen zone II-zone encloses a coring gap of almost 100
 310 ka. Pollen zone III (315.56–305.4 mbsf: 4.41–4.26 Ma, 13-14 samples) shows a stepwise increase of the pollen and spores
 311 concentration with its maximum at 4.3 Ma. The concentration is strongly controlled by Podocarpaceae pollen which account
 312 for up to 44% of the pollen sum in this zone. The pollen of lowland rainforest, lower montane forest, páramo, indicators of
 313 humid conditions, and Fe/K show decreased-lower percentages-values than in compared to zone II. Broad range taxa show
 314 some larger fluctuations. The upper montane forest pollen has its maximum extent of this zone (48%) at 4.28 Ma due to the
 315 high percentage of Podocarpaceae. If the Podocarpaceae pollen are excluded from the upper montane forest, the representation
 316 of this vegetation belt shows the same pattern of decline as that of the lower montane forest and lowland rainforest. In pollen
 317 zone IV (304.75–301.3 mbsf: 4.25–4.12 Ma, 8 samples), the pollen and spores concentration decreases sharply after 4.24 Ma.
 318 The pollen percentage of lower montane forest increases. The percentage of fern spores is at its maximum in this zone.
 319 Percentages of páramo, upper montane forest, broad range taxa, indicators of humid conditions, and the Fe/K ratio remain
 320 similar as in zone III. The percentage of lowland rainforest pollen goes through frequent and large fluctuations.



321 Figure 5. Comparison of the palynomorph percentages (based on total pollen and spores) of Podocarpaceae and the different
 322 vegetation belts between 2 Holocene samples (black) and Pliocene samples between 4.7-4.2 Ma (box-whisker plots).
 323

325 3.12 Modern vs. Pliocene pollen assemblages

326 Two samples from the top of ODP Hole 1239B have been analyzed to facilitate a comparison of the recent palynological signal
 327 with modern vegetation (Fig. 5 and Supplementary Figure). Although there is no detailed age control on these
 328 surface/subsurface samples, a Holocene age can be assigned based on the benthic oxygen isotope record (Rincon-Martinez et
 329 al., 2010). Fifty-one different palynomorph types were recognized, including 29 pollen and 22 fern spore types. The samples
 330 are characterized by low pollen and spore concentrations of 685 and 465 grains/cm³, respectively. Indicators of humid
 331 conditions show intermediate values. Herbs and grass pollen are very abundant with 20–26%, but tree and shrub pollen
 332 decreased to 35–46% compared to the early Pliocene interval. Broad range taxa reach their maximum abundance with 26–
 333 27%. Lowland rainforest and páramo pollen have similar representations as in the Pliocene, whereas the lower and upper

montane forest pollen reach their lowest percentages. When compared to the Pliocene pollen composition, some floristic differences are seen. During the Holocene *Podocarpus* is replaced by *Alnus* as the most abundant upper montane forest tree, although *Podocarpus* was still abundant during the glacial (González et al. 2010) whereof the most prominent is the replacement of Podocarpaceae as the most abundant upper montane forest trees by *Alnus*. Another notable difference is the presence of *Rhizophora* pollen in one of the core top samples, whereas it is completely absent in the early Pliocene interval.

3.3 Description of the páramo

The pollen spectrum from the páramo at ODP Site 1239 includes three different taxa which are mainly confined to the páramo: the pollen type *Polylepis/Acaena*, and the fern spores *Huperzia* and *Jamesonia/Eriosorus* (Fig. 6). Other taxa, which are characteristic of páramos, but cannot be exclusively attributed to this ecosystem because of their broad range occurrence, were not included in the páramo sum (e.g. Asteraceae, Poaceae, Ericaceae). The record shows the continuous presence of páramo vegetation since at least 6 Ma. The summed páramo sum-pollen constitutes up to 79% of the total pollen and spore sum, with the highest fractions found at 4.24 and 4.61 Ma the beginning of the record (6 Ma), and the lowest fractions around 4.23 and 4.59 Ma, at ca. 3.75 Ma and during the late Pleistocene (Figs. 4 and 6). The pollen and spores types constituting the páramo show similar trends (Fig. 5), which supports the assumption of their common provenance.

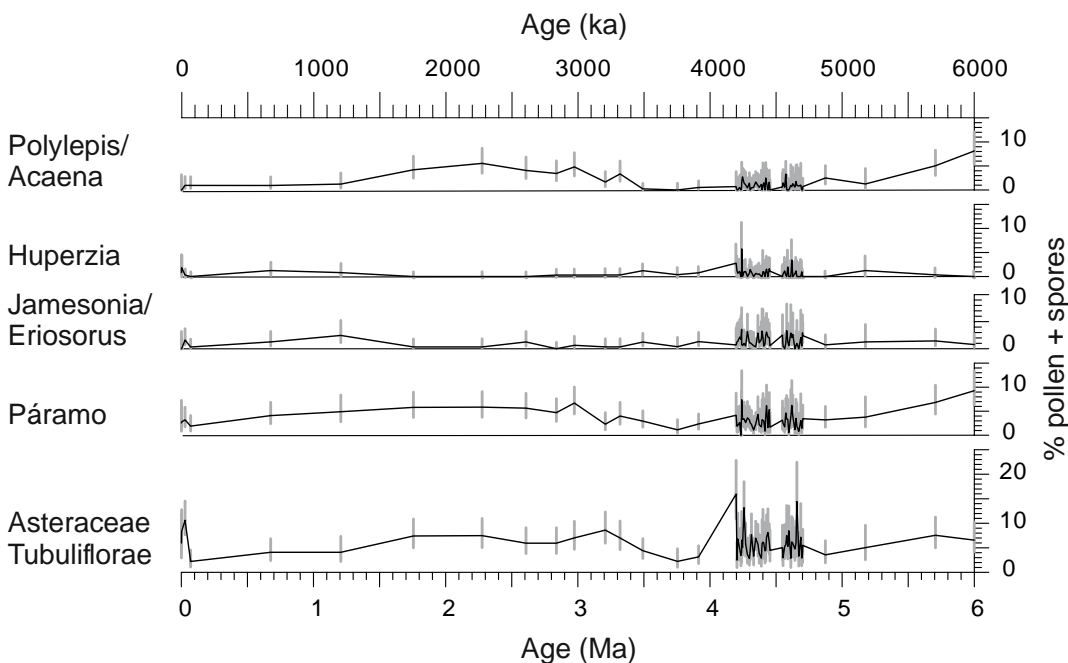


Figure 6. Palynomorph percentages of páramo indicators and Asteraceae Tubuliflorae (excluding *Ambrosia/Xanthium* T) of the past 6 Ma indicating the presence of páramo vegetation at least since the late Miocene. 95% confidence intervals (grey bars) after Mahler (1972). Ages after Tiedemann et al. (2007) and Mix et al (2003). Figure 5: Development of the páramo. Páramo sum with 95% confidence intervals (grey shading). Asteraceae Tubuliflorae sum excluding *Ambrosia/Xanthium* type for comparison. Ages are from Tiedemann et al. (2007). Break of axis represents a hiatus between 4.45 and 4.55 Ma.

4 Discussion

4.31 Fe/K as a tracer for changes in fluvial runoff

The Fe/K ratio has been shown to be a suitable tracer to distinguish between terrigenous input of slightly weathered material from drier regions from and highly weathered material from humid tropical latitudes. Sediments from deeply chemically weathered terrains have higher iron concentrations compared to the more mobile potassium (Mulitza et al., 2008). Before paleoclimatic interpretations can be made based on elemental ratios, other processes which possibly influence the distribution

of Fe/K in marine sediments should be examined, like changes of the topography of Andean river drainage basins, the input of mafic rock material, or diagenetic Fe remobilization (Govin et al., 2012). For northeastern South America it was shown that during the middle Miocene, uplift of the Eastern Andean Cordillera led to changes in the drainage direction of the Orinoco and Magdalena rivers and to the formation of the Amazon River (Hoorn, 1995; Hoorn et al., 2010). If a similar temporal history of uplift and changing drainage patterns is assumed for the western Andean Cordillera, the large-scale patterns of the present topography and river drainage basins should have been in place by the early Pliocene. Therefore, the main direction of fluvial transport of Fe should have been similar to today. Diagenetic alteration was shown not to affect Fe concentrations at Site 1239 (Rincon-Martinez, 2013). The Fe/K ratio therefore seems to be an adequate tracer of fluvial input at this study site. The trend of Fe/K is similar to the pattern of humidity inferred from the pollen spectrum, showing the highest values around 4.46 Ma, thus supporting the hydrological interpretation of the pollen record.

4.21 The Holocene as modern reference

In order to better understand the source areas and transport ways of pollen grains to the sediments, we make a comparison of the results of our two Holocene samples (Supplementary Figure) with that of another pollen record retrieved from the Carnegie Ridge southeast of ODP Site 1239 (TR 163-38, Fig. 2) reflecting rainfall and humidity variation of the late Pleistocene (González et al. 2006). Holocene samples of Site 1239 gave similar results showing extensive open vegetation (indicated by pollen of Poaceae, Cyperaceae, Asteraceae) and maximum relative abundance of fern spores although concentration is low (González et al., 2006). As also indicated by the elemental ratios, fluvial transport of pollen predominates in this area (González et al., 2006; Ríncón-Martínez, 2013). This is understandable, as both ocean currents and wind field do not favor transport from Ecuador to Site 1239 (Fig. 2).

~~The core top samples indicate an expansion of broad range taxa and open vegetation, which happened on the expense of the montane forest being strongly diminished compared to the Pliocene situation. This together with the relatively low pollen concentrations would suggest drier conditions. Although there is no detailed age control on these surface/subsurface samples, a Holocene age can be assigned based on the benthic oxygen isotope record (Rincón-Martínez et al., 2010). A Holocene pollen record from nearby core TR 163-38 has high similarity to the core top samples in its youngest part, showing increased open vegetation (Poaceae, Cyperaceae, Asteraceae), low percentages of *Rhizophora*, maximum percentages of fern spores, and low pollen and spores concentrations (González et al., 2006).~~ Despite the expansion of open vegetation, González et al. (2006) interpreted this record to reflect permanently humid conditions, with disturbance processes caused by human occupation and more intense fluvial dynamics. The relatively high percentage of indicators of humid conditions in ~~our~~the core top samples compared to pollen zones III and IV in the early Pliocene would be in agreement with this interpretation. The core top samples from ODP hole 1239B and the most recent part of core TR 163-38 are taken as a basis for the hydrological interpretation of the Pliocene pollen record.

4.23 Climatic implications of vegetation change

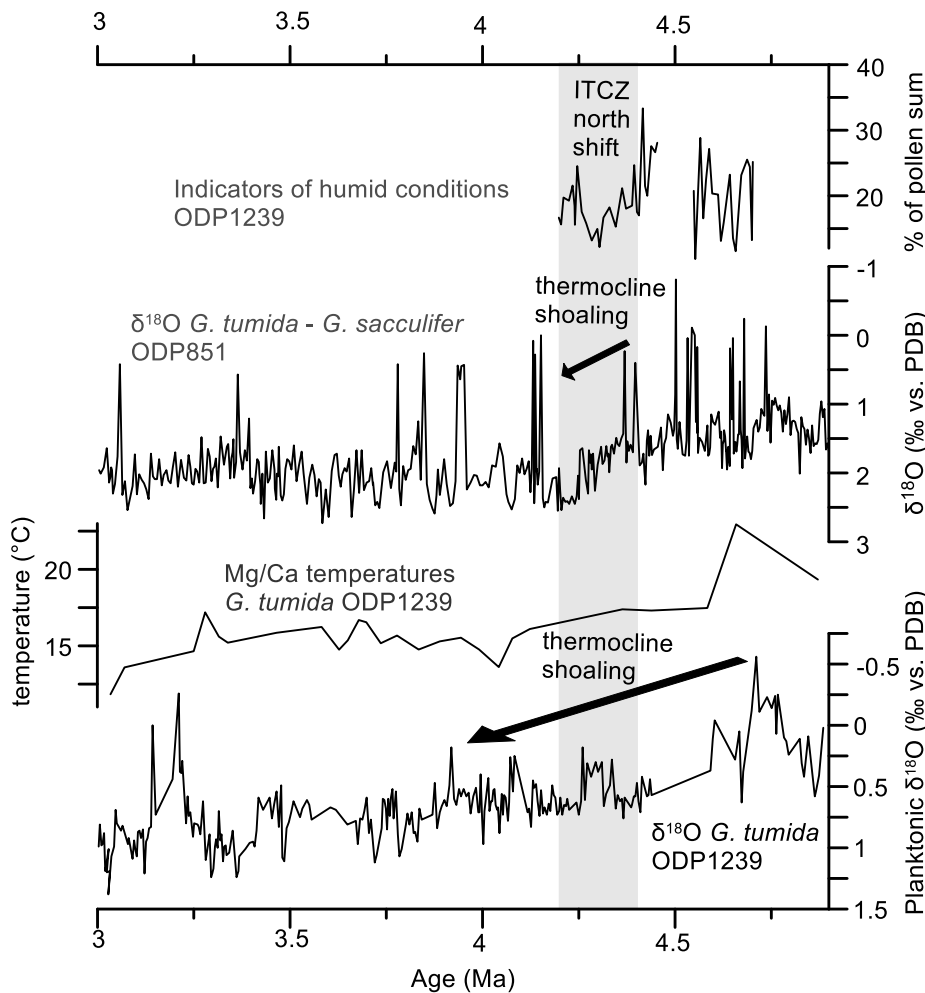
The presented marine palynological record provides new information on floristic and vegetation changes occurring along diverse ecological and climatic gradients through the early Pliocene. The consistently high percentage of tree and shrub pollen, compared to a low percentage of herbs and grass pollen (< 25%) suggests the predominance of forests and the nearly absence of open grasslands (~~below the forest line~~apart from páramo) during the early Pliocene. Moreover, the very low percentage of dry indicators (Amaranthaceae) suggests the absence of persisting drought conditions and supports the idea of a rather stable and humid climate that favored a closed forest cover. This is in good accordance with Pliocene climate models suggesting warmer and wetter conditions on most continents, which led to expansions of tropical forests and savannas at the expense of deserts, ~~for instance in Africa~~ (Salzmann et al., 2011). During the early Pliocene, no profound changes in the vegetation occur. All altitudinal vegetation belts are already present, with varying ratios, ~~and only pollen percentages of lowland rainforest rise~~

403 from almost absent to 6%. The representation of lowland rainforest goes through the most prominent development, from being
404 almost absent to about 6% of the pollen sum.

405 Shifts in the vegetation are driven by various parameters such as temperature, precipitation, CO₂, radiation, and any
406 combination thereof. However, a hint to which parameter has strongest influence on the vegetation might be given by the
407 pattern of expansion and retreat of different vegetation belts. Hooghiemstra and Ran (1994) indicate that if temperature were
408 the dominant driver of vegetation change, altitudinal shifting of vegetation belts would lead to increase in the representation
409 of one at the cost of another. We hardly see such a pattern in our record with the possible exception in zone III where the trends
410 between pollen percentages of páramo and those of upper montane forest (without Podocarpaceae) are reversed (Section 4.3.2;
411 Fig. 8). However, the more general pattern indicates parallel changes in the representation of the forest belts suggesting that
412 not temperature but humidity had the stronger effect on the Pliocene vegetation of Ecuador. Shifts in vegetation are caused by
413 changes of various parameters such as temperature, precipitation, CO₂, radiation, and they can rarely be explained by a single
414 parameter but are a result of their complex interplay. It is therefore challenging to find the parameter which has the strongest
415 influence on vegetation. All altitudinal vegetation belts (if Podocarpaceae are excluded) show a similar pattern of expansion
416 and retreat over time, with an increase in pollen zone I, a maximum in pollen zone II, retreat in pollen zone III, and another
417 maximum in pollen zone IV. It is known from other Andean pollen records (e.g. Hooghiemstra and Ran (1994)) that vegetation
418 belts forced by temperature follow a pattern of opposing expansion and retreat. Such a pattern is seen here in the upper montane
419 forest and the páramo belt (Fig. 5), but the more general pattern which comprises all vegetation belts seems to reflect changes
420 in hydrology rather than temperature. In this respect, a synchronous increase/decrease in all vegetation belts is interpreted to
421 reflect more humid/less humid conditions.

422 **4.23.1 Development of the coastal vegetation**

423 Early Pliocene Ppollen zones I and IV show an expansion of coastal desert herbs (Amaranthaceae, Fig. S1 Supplementary
424 Figure), which coincides with low SSTs-sea-surface temperatures at ODP Site 846 in the EEP, suggesting an influence of the
425 Peru-Chile Humboldt Current (continuation of the Humboldt Current) on the coastal vegetation of southern Ecuador.
426 Remarkably, the lowland rainforest and the coastal desert herbs follow a similar trend. This seems odd at the first glance, but
427 a possible mechanism to explain this pattern would invoke effects of El Niño, the warm phase of ENSO. The main transport
428 agent for pollen in this region are rivers, but in the coastal desert area of southern Ecuador and northern Peru, fluvial discharge
429 rates are low (Milliman and Farnsworth, 2011). Therefore, pollen might be retained on land until an El Niño event causes
430 severe flooding in the coastal areas (Rodbell et al., 1999) and episodically fills the rivers which transport the pollen to the
431 ocean. The Such possible effects of El Niño seem to be strongest in pollen zones I and IV where pollen percentages of the
432 lowland rainforest and coastal desert herbs, but also the upper montane forest, fluctuate most strongly. The lowland rainforest
433 of the coastal plain of Ecuador and western Colombia further north is within the present-day range of the ITCZ, and expanded
434 from 4.7 Ma onwards possibly due to a southwards displacement of the mean latitude of the ITCZ (unpublished data from the
435 earliest Pliocene show that the percentage of lowland rainforest before 4.7 Ma was very low Figs. 3 and 4).



437
 438 **Figure 67.** Percentages of indicators of humid conditions (ODP Site 1239, this study), *G. tumida* – *G. sacculifer* difference in $\delta^{18}\text{O}$
 439 from ODP Site 851 in the eastern equatorial Pacific (Cannariato and Ravelo, 1997), and *G. tumida* Mg/Ca temperatures and $\delta^{18}\text{O}$
 440 from ODP Site 1239 (Steph, 2005; Steph et al., 2010). Grey shading marks the period of thermocline shoaling at ODP Site 851 and
 441 ITCZ north shift.

442
 443 ~~The development of the lowland rainforest also seems to be related to changes in eustatic sea level. High sea levels~~
 444 ~~(Miller et al., 2005) coincide with peaks of the lowland rainforest in pollen zones II and IV.~~ **4.23.2 Development of the**
 445 **montane vegetation**

446 Podocarpaceae strongly dominate the pollen spectrum in general. ~~However, the trend in pollen percentages of Podocarpaceae~~
 447 ~~divert from that of the other pollen taxa, which may be explained by additional transport of Podocarpaceae pollen by wind~~
 448 ~~but the development of the pollen values is decoupled from that of all other taxa. This behavior can be explained if a different~~
 449 ~~transport agent is considered.~~ The high pollen production of Podocarpaceae and their specialized morphology (Regal, 1982)
 450 facilitate their eolian transport. In contrast, pollen from most other taxa is predominantly fluviually transported (González et al.,
 451 2006), therefore exhibiting a different pattern where high pollen concentrations correspond to high fluvial discharge in the
 452 source area. ~~The e~~Eolian transport of Podocarpaceae explains the high pollen concentrations in pollen zone III, which occur
 453 despite less humid conditions compared to pollen zones II and IV. The increased eolian transport at 4.63 Ma and between 4.4
 454 and 4.25 Ma is proposed here to be the result of an intensification of the easterly trade winds. ~~Increase in trade wind strength~~
 455 ~~at 4.4 Ma would be in line with a shift in the locus of maximum opal accumulation rates in the ocean associated with a shift in~~
 456 ~~nutrient availability from ODP Site 850 to ODP Site 846 nearer to the continent (positions shown in Fig. 2) (Farrell et al.,~~
 457 ~~1995). Dynamic modelling indicates that stronger easterlies would cause shoaling of the EEP thermocline (Zhang et al., 2012),~~
 458 ~~which took place between 4.8 and 4.0 Ma (Fig. 7; Steph et al., 2006a) Stronger easterlies also caused the shoaling of the~~
 459 ~~thermocline in the EEP, as shown by models with a dynamic atmosphere (Zhang et al., 2012). The thermocline in the EEP~~

shoaled between 4.8 and 4.0 Ma (Steph et al., 2006a, Fig. 6). Related to this process, a critical step of easterly trade wind intensification, indicated by increased eolian transport of Podocarpaceae pollen, occurred between 4.4 and 4.25 Ma. Another noteworthy oceanographic change occurred at 4.4 Ma in the EEP. Farrell et al. (1995) described a shift in the locus of maximum opal accumulation rates from ODP Site 850 to ODP Site 846 (Galápagos region), caused by a shift in the availability of nutrients, which is possibly related to increased trade wind strength after 4.4 Ma. Besides being influenced by hydrological changes and wind strength, the upper montane forest and the páramo also respond to temperature changes. Expansions of the upper montane forest combined with retreats of the páramo coincide with higher sea surface temperatures in the EEP (ODP Site 846, Fig. 7). Warmer atmospheric temperatures cause an expansion of the upper montane forest to higher altitudes, resulting in a reduction of the area occupied by páramo and therefore the decline of páramo pollen. On the other hand, higher sea surface temperatures cause higher evaporation and thus higher orographic precipitation in the western Andean Cordillera which might also play a role.

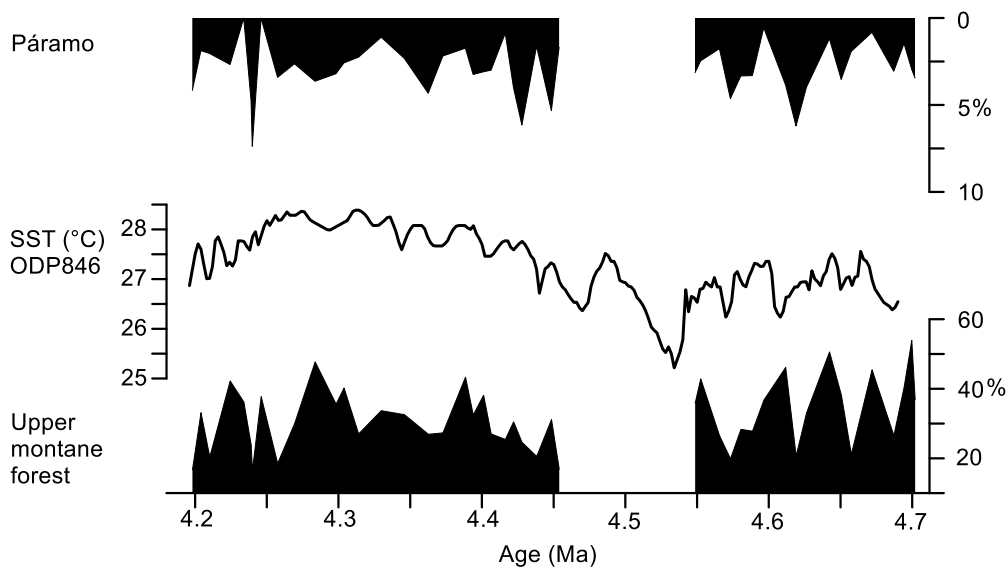


Figure 78. Sums Pollen percentages of upper montane forest and páramo, and UK'37 sea-surface temperatures (SST) of ODP site 846 in the eastern equatorial Pacific (Lawrence et al., 2006).

4.3 Fe/K as a tracer for changes in fluvial runoff

The Fe/K ratio has been shown to be a suitable tracer to distinguish terrigenous input of slightly weathered material from drier regions from highly weathered material from humid tropical latitudes. Sediments from deeply chemically weathered terrains have higher iron concentrations compared to the more mobile potassium (Mulitza et al., 2008). Before paleoclimatic interpretations can be made based on elemental ratios, other processes which possibly influence the distribution of Fe/K in marine sediments should be examined, like changes of the topography of Andean river drainage basins, the input of mafic rock material, or diagenetic Fe remobilization (Govin et al., 2012). For northeastern South America it was shown that during the middle Miocene, uplift of the Eastern Andean Cordillera led to changes in the drainage direction of the Orinoco and Magdalena rivers and to the formation of the Amazon River (Hoorn, 1995; Hoorn et al., 2010). If a similar temporal history of uplift and changing drainage patterns is assumed for the western Andean Cordillera, the large scale patterns of the present topography and river drainage basins should have been in place by the early Pliocene. Therefore, the main direction of fluvial transport of

491 ~~Fe should have been similar to today. Diagenetic alteration was shown not to affect Fe concentrations at Site 1239 (Rincon-~~
492 ~~Martinez, 2013). The Fe/K ratio therefore seems to be an adequate tracer of fluvial input at this study site. The trend of Fe/K~~
493 ~~is similar to the pattern of humidity inferred from the pollen spectrum, showing the highest values around 4.46 Ma, thus~~
494 ~~supporting the hydrological interpretation of the pollen record.~~

495 4.4 Development of the páramo and implications for Andean uplift

496 In order to use [the existence of](#) páramo vegetation as an indicator for Andean elevation, the altitudinal restriction of the páramo
497 taxa to environments above the forest line is a prerequisite. Although no ~~true taxa restricted to páramo~~ ~~endemies occurred were~~
498 ~~identified~~ in the marine samples, or rather, they could not be identified due to the lack of genus-level morphological distinction
499 (especially *Espeletia* from the Asteraceae and some Poaceae, e.g. *Festuca*), several taxa are mainly confined to high Andean
500 environments. Dwarf trees of *Polylepis* typically form patches above the forest line and its natural altitudinal range is thought
501 to occur between a lower limit which forms the transition to other forest types and up to 5000 m [in Bolivia](#) (Kessler, 2002).
502 *Huperzia* occurs in montane forests as epiphytes and with terrestrial growth form in the páramo (Sklenar et al., 2011).
503 *Jamesonia* and *Eriosorus* are both found in cool and wet highlands, with most species being found between 2200 and 5000 m
504 (Sánchez-Baracaldo, 2004). Asteraceae are not restricted to the páramo, but their occurrence in the montane forest and in the
505 lowland rainforest of the Pacific coast is scarce (Behling et al., 1998). With a contribution of up to 16% of the pollen sum,
506 their source area can be attributed mainly to the páramo. Additionally, the fluctuations are similar to the other páramo taxa
507 [\(Fig. 6\)](#), which is another indication for their common source area.

508 The pollen record shows a continuous existence of páramo vegetation ~~without changes in composition~~. During the warm
509 Pliocene, the upper montane forest is assumed to have extended to similar or even higher altitudes as today. Despite this
510 upward expansion of the upper montane forest, the páramo was still present, which implies that the western Cordillera of the
511 ~~northern Ecuadorian~~ Andes had already gone through substantial uplift by that time. Furthermore, the pollen record has a large
512 montane signature, which would not be the case if the Andes had reached less than half of their modern height by the early
513 Pliocene (Coltorti and Ollier, 2000). The upper montane forest which constitutes up to 60% of the pollen sum shows that
514 montane habitats with the corresponding altitudinal belts were already existent. These findings suggest an earlier [uplift history](#)
515 ~~for the western Cordillera of the Northern Andes and according~~ development of the high Andean páramo ecosystem than
516 previously inferred from palynological studies of the eastern Cordillera in Colombia (Hooghiemstra et al., 2006; Van der
517 Hammen et al., 1973). This might also be an indication that the uplift history of the western Cordillera of Ecuador is temporally
518 more closely related to the uplift of the Central Andes where a major phase of uplift occurred between 10 and 6 Ma (Garziona
519 et al., 2008). In another recent palynological study, the arrival of palynomorphs from the páramo in sediments of the Amazon
520 ~~fan~~ has been documented since 5.4 Ma (Hoorn et al., 2017). Since the Amazon has its westernmost source in Peru, this signal
521 might be related to the uplift of the Central Andes. These new records [agree with paleoclimatic studies showing that modern](#)
522 [type precipitation patterns have likely been in place since the middle Miocene](#) (Barnes et al., 2012; Hoorn et al., 2010;
523 Kaandorp et al., 2006). ~~Which would have required a significant orographic barrier. High Andean mountains also imply that~~
524 ~~the modern atmospheric circulation with the Andes~~ acting as a climate divide [might thus go as far back as the Mid-Miocene.](#)
525 [However, first earliest evidence for a páramo vegetation is now set as latest Miocene to early Pliocene. has essentially been in](#)
526 ~~place at least since the late Miocene/early Pliocene.~~

527 4.5 Comparing models and proxy data

528 Several studies have suggested the existence of a “permanent El Niño” during the Pliocene (e.g. Fedorov et al., 2006; Wara et
529 al., 2005). El Niño events are characterized by a shift in the Walker circulation, resulting in exceptionally heavy precipitation
530 particularly over the lowlands of central and southern Ecuador (Bendix and Bendix, 2006) and simultaneous below-average
531 rainfall over the northwestern slopes of the Andes (Vuille et al., 2000). A permanent El Niño-like climate state during the early

532 Pliocene would thus have involved permanently humid conditions with high rates of precipitation and fluvial discharge in the
533 lowlands. Such a climate would have favored the persistence of a broad rain forest coverage and precluded the development
534 of the desert that exists in coastal southern Ecuador today. The presented pollen record indeed indicates very humid conditions
535 and the only indicator of dry vegetation is a small percentage of Amaranthaceae pollen. The predicted pattern of expansion of
536 lowland rainforest at the cost of Andean forest during permanent El Niño is not reflected in the pollen record. ~~Instead, all~~
537 ~~altitudinal vegetation belts go through simultaneous shifts of expansion and retreat.~~

538 The hypothesis of a permanent El Niño climate state involving a reduced zonal Pacific ~~SST-sea-surface temperature~~ gradient
539 has recently been questioned as ~~SST-sea-surface temperature~~ reconstructions differ substantially depending on the method.
540 Zhang et al. (2014) claim that a zonal temperature gradient of ~~-ca. 3°C~~ has existed since the late Miocene and even intensified
541 during the Pliocene. Our pollen record instead indicates an influence of periodic El Niño-related variations on the coastal and
542 montane vegetation, especially between 4.7 and 4.55 Ma and between 4.26 and 4.2 Ma, recorded by strong fluctuations in the
543 pollen percentages of coastal and montane vegetation. ~~Our record does not show increased representation of one vegetation~~
544 ~~belt at the cost of another indicating that altitudinal shifts were not extensive and moisture availability might have been an~~
545 ~~important driver of Pliocene vegetation change. Changes in humidity~~~~The overall parallel expansion and retreat of all vegetation~~
546 ~~belts would make a more uniform shift in moisture supply a more likely explanation. Such a shift~~ could be caused by a
547 latitudinal displacement of the ITCZ. A southward displacement of the ITCZ over both Atlantic and Pacific has been proposed
548 as a response to stronger zonal temperature and pressure gradients which developed after the restriction of the Central
549 American Seaway and/or a weakening of Southern Hemisphere temperature gradients (Billups et al., 1999). The timing of the
550 southward shift was narrowed down to 4.4 to 4.3 Ma in this study, based on $\delta^{18}\text{O}$ records of planktonic foraminifera. The
551 pollen record suggests a slightly different timing, with a gradual southwards displacement of the ITCZ between 4.7 Ma and
552 4.42 Ma when the southernmost position was reached. A less humid phase, indicated by a decrease of humid indicators,
553 lowland rainforest pollen, lower montane forest pollen, and the Fe/K ratio, followed between 4.42 and 4.26 Ma where the
554 ITCZ presumably had a slightly more northern position. This phase coincides with the shoaling of the thermocline at ODP Site
555 851 in the eastern equatorial Pacific (Cannariato and Ravelo, 1997, Fig. 6). A southward displacement of the ITCZ during the
556 early Pliocene would also be in accordance with eolian deposition patterns in the EEP which show a latitudinal shift in eolian
557 grain-size and eolian flux between 6 and 4 Ma (Hovan, 1995). The rather small and slow changes in humidity imply that the
558 ITCZ shift was a gradual process, rather than the response to a single threshold. Just like the Central American Seaway was
559 restricted and reopened several times before its definitive closure at around 2.8 Ma (O’Dea et al., 2016), the atmospheric
560 circulation might have adapted gradually in several small steps to these tectonic changes.

561 Numerical models suggesting a northward shift of the ITCZ in response to the closure of the Central American Seaway or the
562 uplift of the northern Andes do not necessarily disagree with an early Pliocene southward shift inferred from proxy data. Both
563 events occurred gradually over several millions of years and despite recent advances in constraining these events, the timing
564 of major phases in the uplift histories are still debated. In the case of the Central American Seaway, the timing of surface water
565 restriction based on diverging salinities in the Caribbean and Pacific ocean, respectively, is well constrained and numerous
566 global oceanographic changes have been associated with it. Possibly these oceanic reorganizations did not directly trigger
567 modifications of the atmospheric circulation ~~(Kaandorp et al., 2006; Hoorn et al., 2010)~~, but critical periods of uplift
568 influencing atmospheric circulation might have occurred earlier. On the other hand, the respective model sensitivity
569 experiments generally only consider isolated changes in single boundary conditions (e.g. closed or open Central American
570 Seaway). Therefore, the effect of those (i.e. a northward shift of the ITCZ) might counteract the general trend of a southward
571 shift since the late Miocene due to a decrease in the hemispheric temperature gradient (e.g. Pettke et al., 2002). Additionally,
572 global coupled models exhibit uncertainties in the representation of ocean–atmosphere feedback and cloud–radiation
573 feedbacks, which are especially strong in the study region (i.e. showing a double ITCZ and an extensive EEP cold tongue (Li
574 and Xie, 2014)). This is problematic also in the light of the high sensitivity of the ITCZ position to slight shifts in the

575 atmospheric energy balance (Schneider et al., 2014). Another aspect to consider is that whereas proxy records record the
576 transient response of the climate system over a limited ~~time~~ period of time, the mentioned model simulations rather follow the
577 overall equilibrium response than do not reproducing a stepwise process of environmental changes, ~~e.g. following the closure~~
578 ~~of the Panama isthmus (i.e. the shoaling of the thermocline at ~4.8–4.0 Ma and the start of the EEP cold tongue at ~4.3–~~
579 ~~3.6 Ma, as according to Lawrence et al. (2006) and Steph et al. (2006a)), but the overall equilibrium response.~~

580 Concerning the uplift of the northern Andes, there is still a large uncertainty about the time when the ~~Eastern~~ Cordilleras
581 reached ~~their~~ current elevation. Moreover, phases of major uplift might have strongly differed regionally. Paleobotanists
582 (e.g. Hooghiemstra et al., 2006; ~~Hoorn et al., 2010~~; Van der Hammen et al., 1973) and some tectonic geologists (e.g. Mora et
583 al., 2008) argued for a rapid rise of the Eastern Cordillera region since 4–6 Ma, while others conclude that this is rather unlikely
584 implying an earlier uplift based on biomarker-based paleotemperatures (e.g. Anderson et al., 2015; Mora-Páez et al., 2016).
585 Possibly the Pliocene oceanic reorganizations did not directly trigger modifications of the atmospheric circulation, which
586 probably was more or less in place (Kaandorp et al., 2006; Hoorn et al., 2010). Critical periods of uplift influencing atmospheric
587 circulation might have occurred earlier (see also above). The estimates for uplift of the ~~w~~Western Cordillera in Ecuador differ
588 even more strongly, and range from rapid exhumation around 13 and 9 Ma based on thermochronology (Spikings et al., 2005)
589 to a recent uplift during the Pliocene and Pleistocene (Coltorti and Ollier, 2000). Our pollen record from the páramo shows
590 that the Western Cordillera of the northern Ecuadorian Andes must have already reached close to modern elevations by the
591 early Pliocene in line with inferences of Hoorn et al. (2017) and Bermúdez et al. (2015). If an early Andean uplift is assumed,
592 the atmospheric response predicted by the model would have occurred earlier, which would also be in agreement with proxy
593 data indicating a northern position of the ITCZ during the late Miocene (Hovan, 1995).

594 Overall, even if the timing and identification of major steps in the shoaling and restriction of the Central American Seaway or
595 in the uplift of the ~~n~~Northern Andes are resolved, the critical threshold for profound changes in atmospheric circulation and
596 climate may have occurred at any time during the tectonic processes. Within the analyzed time window, large changes in
597 atmospheric circulation which have been proposed as a response to the closure of the Central American Seaway (Ravelo et al.,
598 2004) are absent.

599 5 Conclusions

- 600 1) Between 4.7 and 4.2 Ma, a permanently humid climate with broad rainforest coverage existed in western equatorial
601 South America. No evidence was found for a permanent El Niño-like climate state, but strong fluctuations in the
602 vegetation between 4.7 and 4.55 Ma and between 4.26 and 4.2 Ma indicate strong periodic El Niño variability at this
603 time. Hydrological changes between 4.55 and 4.26 Ma are attributed to gradual shifts of the Intertropical Convergence
604 Zone which reached its southernmost position around 4.42 Ma and shifted slightly north afterwards.
- 605 2) The most prominent shift recorded during the early Pliocene is an increase in the representation of the lowland
606 rainforest around 4.5 Ma ~~in the vegetation occurred in the lowland rainforest.~~
- 607 3) Between 4.41 and 4.26 Ma, an increased eolian influx of Podocarpaceae pollen indicates an increased strength of the
608 easterly trade winds, which is presumably related to the shoaling of the EEP thermocline.
- 609 4) Results from proxy data and numerical modelling studies regarding the position of the ITCZ during the early Pliocene
610 are not necessarily contradictory. Considering the temporal uncertainties regarding major steps of CAS closure and
611 uplift of the northern Andes, the proposed northward shift of the ITCZ in response to these events might have occurred
612 much earlier (e.g. during the middle to late Miocene).
- 613 5) The continuous presence of páramo vegetation since 6 Ma implies that by the early Pliocene, the western Cordillera
614 of the northern Ecuadorian Andes had already reached an elevation suitable for the development of vegetation above
615 the upper forest line by the latest Miocene. We present new paleobotanical evidence indicating an earlier development

616 [of páramo vegetation](#) ~~This new paleobotanical evidence points towards an earlier uplift of the northern Andes than~~
617 previously suggested by terrestrial paleobotanical records.

619 Data availability

620 The underlying research data ~~can be accessed~~ are stored in ~~via~~ <https://pangaea.de> PANGAEA as datasets [PANGAEA.884280](https://pangaea.de/PANGAEA.884280),
621 [PANGAEA.891294](https://pangaea.de/PANGAEA.891294) and [PANGAEA.884153](https://pangaea.de/PANGAEA.884153), which are combined in [PANGAEA.884285](https://pangaea.de/PANGAEA.884285)
622 ~~<<https://doi.pangaea.de/10.1594/PANGAEA.884285>>~~.

624 Author contribution

625 L. Dupont and F. Grimmer conceived the idea, and L. Dupont, F. Grimmer and F. Lamy carried out the analyses. F. Grimmer
626 prepared the manuscript with contributions from all co-authors.

628 Competing interests

629 The authors declare that they have no conflict of interest.

631 Acknowledgements

632 This project was funded by the Deutsche Forschungsgemeinschaft (DFG) through the TROPSAP project (DU221/6) and via
633 the DFG Research Center / Cluster of Excellence “The Ocean in the Earth System — MARUM”. The first author thanks
634 GLOMAR – Bremen International Graduate School for Marine Sciences, University of Bremen, Germany, for support. The
635 IODP Gulf Coast Repository (GCR) we acknowledge for their assistance in providing the core samples.

637 References

- 638 Anderson, V. J., Saylor, J. E., Shanahan, T. M., and Horton, B. K.: Paleoelevation records from lipid biomarkers:
639 Application to the tropical Andes, *Geological Society of America Bulletin*, 127, 1604-1616, 2015.
- 640 Balslev, H.: Distribution Patterns of Ecuadorean Plant-Species, *Taxon*, 37, 567-577, 1988.
- 641 Barnes, J. B., Ehlers, T. A., Insel, N., McQuarrie, N., and Poulsen, C. J.: Linking orography, climate, and exhumation
642 across the central Andes, *Geology*, 40, 1135-1138, 2012.
- 643 Bartoli, G., Sarnthein, M., Weinelt, M., Erlenkeuser, H., Garbe-Schönberg, D., and Lea, D. W.: Final closure of
644 Panama and the onset of northern hemisphere glaciation, *Earth and Planetary Science Letters*, 237, 33-44, 2005.
- 645 Behling, H., Hooghiemstra, H., and Negret, A. J.: Holocene history of the Choco Rain Forest from Laguna Piusbi,
646 Southern Pacific Lowlands of Colombia, 1998. 1998.
- 647 Bendix, A. and Bendix, J.: Heavy rainfall episodes in Ecuador during El Nino events and associated regional
648 atmospheric circulation and SST patterns, *Advances in Geosciences*, 6, 43-49, 2006.
- 649 Bendix, J. and Lauer, W.: Die Niederschlagsjahreszeiten in Ecuador und ihre Klimadynamische Interpretation,
650 1992. 1992.
- 651 Billups, K., Ravelo, A. C., Zachos, J. C., and Norris, R. D.: Link between oceanic heat transport thermohaline
652 circulation and the Intertropical Convergence Zone in the early Pliocene Atlantic, *Geology*, 24, 319-322, 1999.
- 653 Bush, M. B. and Weng, C.: Introducing a new (freeware) tool for palynology, *Journal of Biogeography*, 34, 377-
654 380, 2007.
- 655 Cannariato, K. G. and Ravelo, A. C.: Pliocene-Pleistocene evolution of eastern tropical Pacific surface water
656 circulation and thermocline depth, *Paleoceanography*, 12, 805-820, 1997.
- 657 Colinvaux, P., De Oliveira, P. E., and Moreno Patino, J. E.: Amazon Pollen Manual and Atlas, 1999.
- 658 Coltorti, M. and Ollier, C. D.: Geomorphic and tectonic Evolution of the Ecuadorian Andes, *Geomorphology*, 32,
659 1-19, 2000.
- 660 Corredor, F.: Eastward extent of the Late Eocene-Early Oligocene onset of deformation across the northern Andes:
661 constraints from the northern portion of the Eastern Cordillera fold belt, Colombia, *Journal of South American*
662 *Earth Sciences*, 16, 445-457, 2003.

663 Farrell, J. W., Raffi, I., Janecek, T. R., Murray, D. W., Levitan, M., Dadey, K. A., Emeis, K.-C., Lyle, M., Flores, J. A.,
664 and Hovan, S.: Late Neogene Sedimentation Patterns in the eastern equatorial Pacific Ocean, Proceedings of the
665 Ocean Drilling Program, Scientific Results, 138, 1995.

666 Fedorov, A. V., Dekens, P. S., McCarthy, M., Ravelo, A. C., deMenocal, P. B., Barreiro, M., Pacanowski, R. C., and
667 Philander, S. G.: The Pliocene paradox (mechanisms for a permanent El Niño), *Science*, 312, 1485-1489, 2006.

668 Feng and Poulsen, C. J.: Andean elevation control on tropical Pacific climate and ENSO, *Paleoceanography*, 29,
669 795–809, 2014.

670 Flantua, S., Hooghiemstra, H., Van Boxel, J. H., Cabrera, M., González-Carranza, Z., and González-Arango, C.:
671 Connectivity dynamics since the last glacial maximum in the northern Andes a pollen driven framework to assess
672 potential migration. In: *Paleobotany and Biogeography: A Festschrift for Alan Graham in His 80th Year*, W. D.
673 Stevens, O. M. M., P. H. Raven (Ed.), Missouri Botanical Garden Press, St. Louis, 2014.

674 Flohn, H.: A hemispheric circulation asymmetry during Late Tertiary, *Geologische Rundschau*, 70, 725-736, 1981.

675 Garziona, C. N., Hoke, G. D., Libarkin, J. C., Withers, S., MacFadden, B., Eiler, J., Ghosh, P., and Mulch, A.: Rise of
676 the Andes, *Science*, 320, 1304-1307, 2008.

677 Gentry, A. H.: Species richness and floristic composition of Chocó region plant communities, *Caldasia*, 15, 71-91,
678 1986.

679 González, C., Urrego, L. E., and Martínez, J. I.: Late Quaternary vegetation and climate change in the Panama
680 Basin: Palynological evidence from marine cores ODP 677B and TR 163-38, *Palaeogeography, Palaeoclimatology,*
681 *Palaeoecology*, 234, 62-80, 2006.

682 Govin, A., Holzwarth, U., Heslop, D., Ford Keeling, L., Zabel, M., Mulitza, S., Collins, J. A., and Chiessi, C. M.:
683 Distribution of major elements in Atlantic surface sediments (36°N-49°S): Imprint of terrigenous input and
684 continental weathering, *Geochemistry, Geophysics, Geosystems*, 13, n/a-n/a, 2012.

685 Gregory-Wodzicki, K. M.: Uplift history of the Central and Northern Andes: A review, *Geological Society of America*
686 *Bulletin*, 112, 1091-1105, 2000.

687 Grimm, E.: *Tilia and Tiliagraph*, Illinois State Museum, Springfield, 1991. 1991.

688 Groeneveld, J., Hathorne, E. C., Steinke, S., DeBey, H., Mackensen, A., and Tiedemann, R.: Glacial induced closure
689 of the Panamanian Gateway during Marine Isotope Stages (MIS) 95–100, *Earth and Planetary Science Letters*,
690 404, 296-306, 2014.

691 Haug, G. H. and Tiedemann, R.: Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline
692 circulation, *Nature*, 393, 673-676, 1998.

693 Haug, G. H., Tiedemann, R., Zahn, R., and Ravelo, A. C.: Role of Panama uplift on oceanic freshwater balance,
694 *Geology*, 29, 207-210, 2001.

695 Hooghiemstra, H.: *Vegetational and Climatic History of the High Plain of Bogotá, Colombia: A Continuous Record*
696 *of the Last 3.5 Million Years*, A.R. Gantner Verlag K.G., Vaduz, 1984.

697 Hooghiemstra, H. and Ran, E. T. H.: Upper and middle Pleistocene climatic change and forest development in
698 Colombia pollen record Funza II, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 109, 211-246, 1994.

699 Hooghiemstra, H., Wijninga, V. M., and Cleef, A. M.: The Paleobotanical Record of Colombia: Implications for
700 Biogeography and Biodiversity¹, *Annals of the Missouri Botanical Garden*, 93, 297-325, 2006.

701 Hoorn, C.: Andean tectonics as a cause for changing drainage patterns in Miocene northern South America, 1995.
702 1995.

703 Hoorn, C., Bogotá-A., G. R., Romero-Baez, M., Lammertsma, E. I., Flantua, S., Dantas, E. L., Dino, R., do Carmo, D.
704 A., and Chemale Jr, F.: The Amazon at sea: Onset and stages of the Amazon River from a marine record, with
705 special reference to Neogene plant turnover in the drainage basin, *Global and Planetary Change*, 2017. 2017.

706 Hoorn, C. and Flantua, S.: Geology. An early start for the Panama land bridge, *Science*, 348, 186-187, 2015.

707 Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., Sanmartin, I., Sanchez-Meseguer,
708 A., Anderson, C. L., Figueiredo, J. P., Jaramillo, C., Riff, D., Negri, F. R., Hooghiemstra, H., Lundberg, J., Stadler, T.,
709 Sarkinen, T., and Antonelli, A.: Amazonia through time: Andean uplift, climate change, landscape evolution, and
710 biodiversity, *Science*, 330, 927-931, 2010.

711 Hovan: Late Cenozoic Atmospheric Circulation Intensity and climatic history recorded by eolian deposition in the
712 eastern equatorial pacific ocean Leg138, 1995. 1995.

713 Jørgensen, P. M., León-Yáñez, S., and Missouri Botanical Garden.: *Catalogue of the vascular plants of Ecuador =*
714 *Catálogo de las plantas vasculares del Ecuador*, Missouri Botanical Garden Press, St. Louis, Mo., 1999.

715 Kaandorp, R. J. G., Wesselingh, F. P., and Vonhof, H. B.: Ecological implications from geochemical records of
716 Miocene Western Amazonian bivalves, *Journal of South American Earth Sciences*, 21, 54-74, 2006.

717 Kessler, M.: The "Polylepis problem": Where do we stand?, *Ecotropica*, 8, 97-110, 2002.

718 Lawrence, K. T., Liu, Z., and Herbert, T. D.: Evolution of the eastern tropical Pacific through Plio-Pleistocene
719 glaciation, *Science*, 312, 79-83, 2006.

720 Li, G. and Xie, S. P.: Tropical Biases in CMIP5 Multimodel Ensemble: The Excessive Equatorial Pacific Cold Tongue
721 and Double ITCZ Problems, *Journal of Climate*, 27, 1765-1780, 2014.

722 Lunt, D. J., Valdes, P. J., Haywood, A., and Rutt, I. C.: Closure of the Panama Seaway during the Pliocene:
723 implications for climate and Northern Hemisphere glaciation, *Climate Dynamics*, 30, 1-18, 2008.

724 Luteyn, J. L.: *Páramos*, Memoirs of The New York Botanical Garden, 1999.

725 Maher, L. J.: Nomograms for computing 0.95 confidence limits of pollen data, *Review of Palaeobotany and*
726 *Palynology*, 13, 85-93, 1972.

727 Marchant, R., Almeida, L., Behling, H., Berrio, J. C., Bush, M., Cleef, A., Duivenvoorden, J., Kappelle, M., De Oliveira,
728 P., Teixeira de Oliveira-Filho, A., Lozano-Garcia, S., Hooghiemstra, H., Ledru, M.-P., Ludlow-Wiechers, B.,
729 Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O., and Salgado-Labouriau, M.: Distribution and ecology of
730 parent taxa of pollen lodged within the Latin American Pollen Database, *Review of Palaeobotany and Palynology*,
731 121, 1-75, 2002.

732 Marchant, R., Behling, H., Berrio, J. C., Cleef, A., Duivenvoorden, J., Hooghiemstra, H., Kuhry, P., Melief, B., Van
733 Geel, B., Van der Hammen, T., Van Reenen, G., and Wille, M.: Mid- to Late-Holocene pollen-based biome
734 reconstructions for Colombia, *Quaternary Science Reviews*, 20, 1289-1308, 2001.

735 Miller, K. G., Kominz, M. A., Browning, J. V., Wright, J. D., Mountain, G. S., Katz, M. E., Sugarman, P. J., Cramer, B.
736 S., Christie-Blick, N., and Pekar, S. F.: The Phanerozoic record of global sea-level change, *Science*, 310, 1293-1298,
737 2005.

738 Milliman, J. D. and Farnsworth, K. L.: *River discharge to the coastal ocean : a global synthesis*, Cambridge
739 University Press, Cambridge ; New York, 2011.

740 Mix, A., Tiedemann, R., and Blum, P.: *Proceedings of the Ocean Drilling Program, Initial Reports*, 202, 2003.

741 Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J. C., Valencia, V., Ayala, C., Pérez-Angel, L. C., Rondriguez-
742 Parra, L. A., Ramirez, V., and Nino, H.: Middle Miocene closure of the Central American Seaway,
743 *Paleoceanography*, 348, 226-229, 2015.

744 Mora-Páez, H., Mencin, D. J., Molnar, P., Diederix, H., Cardona-Piedrahita, L., Peláez-Gaviria, J.-R., and Corchuelo-
745 Cuervo, Y.: GPS velocities and the construction of the Eastern Cordillera of the Colombian Andes *Geophysical*
746 *Research Letters* Volume 43, Issue 16. In: *Geophysical Research Letters*, 16, 2016.

747 Mora, A., Parra, M., Strecker, M. R., Sobel, E. R., Hooghiemstra, H., Torres, V., and Jaramillo, J. V.: Climatic forcing
748 of asymmetric orogenic evolution in the Eastern Cordillera of Colombia, *GSA Bulletin*, 120, 930-949, 2008.

749 Mulitza, S., Prange, M., Stuetz, J. B., Zabel, M., von Dobeneck, T., Itambi, A. C., Nizou, J., Schulz, M., and Wefer, G.:
750 Sahel megadroughts triggered by glacial slowdowns of Atlantic meridional overturning, *Paleoceanography*, 23,
751 2008.

752 Murillo, M. T. and Bless, M. J. M.: Spores of recent Colombian Pteridophyta I Trilete Spores, *Review of*
753 *Palaeobotany and Palynology*, 1974. 1974.

754 Murillo, M. T. and Bless, M. J. M.: Spores of recent Colombian Pteridophyta II Monolete Spores, *Review of*
755 *Palaeobotany and Palynology*, 1978. 1978.

756 Niemann, H., Brunschön, C., and Behling, H.: Vegetation/modern pollen rain relationship along an altitudinal
757 transect between 1920 and 3185ma.s.l. in the Podocarpus National Park region, southeastern Ecuadorian Andes,
758 *Review of Palaeobotany and Palynology*, 159, 69-80, 2010.

759 O’Dea, A., Lessios, A. H., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A. L., Collins, L. S., de Queiroz,
760 A., Farris, D. W., Norris, R. D., Stallard, R. F., Woodburne, M. O., Aguilera, O., Aubry, M.-P., Berggren, W. A., Budd,
761 A. F., Cozzuol, M. A., Coppard, S. E., Duque-Caro, H., Finnegan, S., Gasparini, G. M., Grossman, E. L., Johnson, K.
762 G., Keigwin, L. D., Knowlton, N., Leigh, E. G., Leonard-Pingel, J. S., Marko, P. B., Pyenson, N. D., Rachello-Dolmen,
763 P. G., Soibelzon, E., Soibelzon, L., Todd, J. A., Vermeij, G. J., and Jackson, J. B. C.: Formation of the Isthmus of
764 Panama, *Science Advances*, 2, 2016.

765 Pettke, T., Halliday, A. N., and Rea, D. K.: Cenozoic evolution of Asian climate and sources of Pacific seawater Pb
766 and Nd derived from eolian dust of sediment core LL44-GPC3, *Paleoceanography*, 17, 2002.

767 Pisias, N.: Paleoclimatology of the eastern equatorial Pacific during the Neogene: Synthesis of Leg 138 drilling
768 results, *Proceedings of the Ocean Drilling Program, Scientific Results*, 138, 5-21, 1995.

769 Ravelo, A. C., Andreasen, D. H., Lyle, M. W., Lyle, A. O., and Wara, M. W.: Regional climate shifts caused by gradual
770 global cooling in the Pliocene epoch, 2004. 2004.

771 Regal, P. J.: *Pollination by Wind and Animals: Ecology of Geographic Patterns*, *Annual Review of Ecology and*
772 *Systematics*, 13, 497-524, 1982.

773 Richter, T. O., van der Gaast, S., Koster, B., Vaars, A., Gieles, R., de Stigter, H. C., de Haas, H., and van Weering, T.
774 C. E.: The Avaatech XRF Core Scanner: Technical description and applications to NE Atlantic sediments. In: *New*
775 *Techniques in Sediment Core Analysis*, Rothwell, R. G. (Ed.), Geol. Soc. Spec. Publ., 2006.

776 Rincon-Martinez, D.: Eastern Pacific background state and tropical South American climate history during the last
777 3 million years., 2013. Fachbereich Geowissenschaften, Universität Bremen, Bremen, 2013.

778 Rincon-Martinez, D., Lamy, F., Contreras, S., Leduc, G., Bard, E., Saukel, C., Blanz, T., Mackensen, A., and
779 Tiedemann, R.: More humid interglacials in Ecuador during the past 500 kyr linked to latitudinal shifts of the
780 equatorial front and the Intertropical Convergence Zone in the eastern tropical Pacific, *Paleoceanography*, 25,
781 2010.

782 Rodbell, D. T., Seltzer, G. O., Anderson, D. M., Abbott, M. B., Enfield, D. B., and Newman, J. H.: An similar to 15,000-
783 year record of El Niño-driven alluviation in southwestern Ecuador, *Science*, 283, 516-520, 1999.

784 Roubik, D. W. and Moreno, P.: Pollen and spores of Barro Colorado Island [Panama], *Monographs in systematic*
785 *botany from the Missouri Botanical Garden*, 36, 1991.

786 Salzmann, U., Williams, M., Haywood, A. M., Johnson, A. L. A., Kender, S., and Zalasiewicz, J.: Climate and
787 environment of a Pliocene warm world, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 309, 1-8, 2011.

788 Sánchez-Baracaldo, P.: Phylogenetics and biogeography of the neotropical fern genera *Jamesonia* and *Eriosorus*
789 (Pteridaceae), *American Journal of Botany*, 91, 274-284, 2004.

790 Schneider, T., Bischoff, T., and Haug, G. H.: Migrations and dynamics of the intertropical convergence zone,
791 *Nature*, 513, 45-53, 2014.

792 Seilles, B., Goni, M. F. S., Ledru, M. P., Urrego, D. H., Martinez, P., Hanquiez, V., and Schneider, R.: Holocene land-
793 sea climatic links on the equatorial Pacific coast (Bay of Guayaquil, Ecuador), *Holocene*, 26, 567-577, 2016.

794 Sklenar, P., Duskova, E., and Balslev, H.: Tropical and Temperate: Evolutionary History of Paramo Flora, *Bot Rev*,
795 77, 71-108, 2011.

796 Sklenar, P. and Jorgensen, P. M.: Distribution patterns of Paramo Plants in Ecuador, *Journal of Biogeography*, 26,
797 681-691, 1999.

798 Spikings, R. A., Winkler, W., Hughes, R. A., and Handler, R.: Thermochronology of allochthonous terranes in
799 Ecuador: Unravelling the accretionary and post-accretionary history of the Northern Andes, *Tectonophysics*, 399,
800 195-220, 2005.

801 Steph, S.: Pliocene Stratigraphy and the impact of Panama Uplift on changes in caribbean and tropical east pacific
802 upper ocean stratification, 2005. 2005.

803 Steph, S., Tiedemann, R., Groeneveld, J., Sturm, A., and Nürnberg, D.: Pliocene Changes in Tropical East Pacific
804 Upper Ocean Stratification: Response to Tropical Gateways?, *Proceedings of the Ocean Drilling Program, Scientific*
805 *Results*, 202, 2006a.

806 Steph, S., Tiedemann, R., Prange, M., Groeneveld, J., Nurnberg, D., Reuning, L., Schulz, M., and Haug, G. H.:
807 Changes in Caribbean surface hydrography during the Pliocene shoaling of the Central American Seaway,
808 *Paleoceanography*, 21, 2006b.

809 Steph, S., Tiedemann, R., Prange, M., Groeneveld, J., Schulz, M., Timmermann, A., Nürnberg, D., Rühlemann, C.,
810 Saukel, C., and Haug, G. H.: Early Pliocene increase in thermohaline overturning: A precondition for the
811 development of the modern equatorial Pacific cold tongue, *Paleoceanography*, 25, n/a-n/a, 2010.

812 Takahashi, K. and Battisti, D. S.: Processes Controlling the Mean Tropical Pacific Precipitation Pattern. Part I: The
813 Andes and the Eastern Pacific ITCZ, *Journal of Climate*, 20, 3434-3451, 2007.

814 Tiedemann, R., Sturm, A., Steph, S., Lund, S. P., and Stoner, J. S.: Astronomically calibrated timescales from 6 to
815 2.5 Ma and benthic isotope stratigraphies, sites 1236, 1237, 1239, and 1241, *Proceedings of the Ocean Drilling*
816 *Program, Scientific Results*, 202, 2007.

817 Tjallingii, R., Röhl, U., Kölling, M., and Bickert, T.: Influence of the water content on X-ray fluorescence core-
818 scanning measurements in soft marine sediments, *Geochemistry, Geophysics, Geosystems*, 8, 2007.

819 Twilley, R. R., Cárdenas, W., Rivera-Monroy, V. H., Espinoza, J., Suescum, R., Armijos, M. M., and Solórzano, L.:
820 The Gulf of Guayaquil and the Guayas River Estuary, Ecuador. In: *Coastal Marine Ecosystems of Latin America*,
821 Seeliger, U. and Kjerfve, B. (Eds.), Springer, Heidelberg, 2001.

822 Van der Hammen, T.: The Pleistocene Changes of Vegetation and Climate in Tropical South America, *Journal of*
823 *Biogeography*, 1, 3-26, 1974.

824 Van der Hammen, T., Werner, J. H., and van Dommelen, H.: Palynological record of the upheaval of the Northern
825 Andes: a study of the Pliocene and Lower Quaternary of the Colombian early evolution of its high-Andean biota,
826 *Review of Palaeobotany and Palynology*, 16, 1-122, 1973.

827 Vuille, M., Bradley, R. S., and Keimig, F.: Climate variability in the Andes of Ecuador and its relation to tropical
828 Pacific and Atlantic Sea surface temperature anomalies, *Journal of Climate*, 2000. 2000.
829 Wara, M. W., Ravelo, A. C., and Delaney, M. L.: Permanent El Nino-like conditions during the Pliocene warm
830 period, *Science*, 309, 758-761, 2005.
831 Zhang, X., Prange, M., Steph, S., Butzin, M., Krebs, U., Lunt, D. J., Nisancioglu, K. H., Park, W., Schmittner, A.,
832 Schneider, B., and Schulz, M.: Changes in equatorial Pacific thermocline depth in response to Panamanian seaway
833 closure: Insights from a multi-model study, *Earth and Planetary Science Letters*, 2012. 76-84, 2012.
834 Zhang, Y. G., Pagani, M., and Liu, Z.: A 12-million-year temperature history of the tropical Pacific Ocean, *Science*,
835 344, 84-87, 2014.

836
837
838
839
840
841
842
843
844
845
846
847
848
849
850
851
852
853
854
855
856
857
858
859
860

861
862
863
864
865
866
867
868
869
870

Table 1: List of identified pollen and spore taxa in marine ODP Holes 1239A (Pliocene samples) and 1239B (core top samples, taxa in grey occurred only in core top samples) and grouping according to their main ecological affinity (Flantua et al., 2014; Marchant et al., 2002).

Páramo	Upper montane forest	Lower montane forest	Lowland rainforest	Broad-range taxa	Humid indicators
<i>Polylepis/Acaena</i>	Podocarpaceae	Urticaceae/ Moraceae	<i>Arecaceae</i>	Poaceae	Cyperaceae
<i>Jamesonia/Eriosorus</i>	<i>Hedyosmum</i>	<i>Erythrina</i>	<i>Polypodiaceae</i>	Cyperaceae	<i>Ranunculus</i>
<i>Huperzia</i>	<i>Clethra</i>	<i>Alchornea</i>	<i>Pityrogramma</i> <i>Pteris altissima</i> <i>T</i>	Fabuliflorae (Asteraceae)	<i>Hedyosmum</i>
<i>Ranunculus</i>	<i>Myrica</i>	<i>Styloceras</i> <i>T</i>	<i>Wallichia</i>	Amaranthaceae	<i>Cec</i>
<i>Draba</i>	Acanthaceae	Malpighiaceae		Rosaceae	<i>Pachira</i>
<i>Sisyrinchium</i>	Melastomataceae	Cyatheaceae		<i>Ambrosia</i> / <i>Xanthium</i>	<i>Myrica</i>
<i>Cystopteris diaphana</i> <i>T</i>	<i>Daphnopsis</i>	<i>Vernonia</i> <i>T</i>		Ericaceae	Malpighiaceae
	<i>Boeconia</i>	<i>Pteris grandifolia</i> <i>T</i>		<i>Artemisia</i>	Cyatheaceae

<i>Myrsine</i>	<i>Pteris podophylla</i> <i>T</i>	<i>Ulex</i>	<i>Selaginella</i>
<i>Lophosoria</i>	<i>Saccotoma elegans</i> <i>T</i>	<i>Thevetia</i>	<i>Pityrogramma</i> <i>Pteris altissima</i> <i>T</i>
<i>Elaphoglossum</i>	<i>Thelypteris</i>	<i>Salacia</i>	<i>Hymenophyllum</i> <i>T</i>
<i>Hypolepis hostilis</i> <i>T</i>	<i>Ctenitis subincisa</i> <i>T</i>	Bromeliaceae	<i>Thelypteris</i>
<i>Grammitis</i>		Malvaceae	<i>Ctenitis subincisa</i> <i>T</i>
<i>Dodonaea viscosa</i>		Euphorbiaceae	<i>Alnus</i>
<i>Alnus</i>		Liliaceae	<i>Cystopteris diaphana</i> <i>T</i>
		Lycopodiaceae—excl. <i>Huperzia</i> <i>Selaginella</i>	
		<i>Hymenophyllum</i> <i>T</i>	
		<i>Calandrinia</i>	