

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

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Review Report by Henry Hooghiemstra and Suzette Flantua

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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

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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

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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,

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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).

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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).

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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 'paramo' 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

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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

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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.

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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

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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' ?

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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-

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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.

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