

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):

"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. 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 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

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 Histrory and Archaobotany, 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 Humbold 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

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 form the low-land 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

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 indicarion 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)

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, esporodermo 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; Ríncon-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

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.

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,

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 fov) 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

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 Ríncon-Martínez 2013, Sanchez-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. 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' cold 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.

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. Pylanology 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:

C23

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