

Reviewer #3 (Paula A. Rodríguez-Zorro)

The manuscript presented by Akabane et al., presents a synthesis of how vegetation and fire regimes in the Neotropics have responded to climatic changes over the last 21,000 years in seven subregions of the Neotropics. The authors used a modern analysis of vegetation distribution and fire activity in relation to current climatic conditions, complemented by a compilation of 243 vegetation and 127 fire records to assess changes over the past 21 ka BP.

The manuscript is well-structured and comprehensible, offering a significant contribution to the understanding of long-term ecosystem dynamics in the regions studied. Although there is a scarcity of paleo records in some areas, this research is a good example of the importance of databases and open data in enhancing our understanding of Neotropical ecosystems, and it calls for additional research to address the existing knowledge gaps.

Response #1. We thank Paula A. Rodríguez-Zorro very much for her evaluation of our manuscript.

GENERAL COMMENTS

The title proposed by the authors “Vegetation and fire regimes in the Neotropics over the last 21,000 years” suggest an extensive examination of the entire neotropical region. However, this study is restricted to seven specific subregions, omitting the northern Andes, parts of Bolivia and Chile, and large portions of Brazil and Argentina. This selection was partly due to data availability, yet it resulted in a focus on these seven subregions rather than a comprehensive analysis of the Neotropics.

Response #2. We appreciate the observation regarding the generality implied by our title. While it is true that our study focuses on seven subregions, we would like to emphasize that these regions collectively represent by far most of the pollen and charcoal records currently available from the Neotropics, covering a substantial portion of the region. Therefore, we believe that the chosen regions still allow us to draw meaningful conclusions about continental-scale vegetation and fire regime dynamics. Consequently, we feel that the title remains appropriate, even if it does not capture every local detail of the entire region.

In the section on vegetation settings, the authors provide a detailed description of the selected subregions, emphasizing the primary climatic drivers, such as the ITCZ, SASM, and ENSO. However, the analysis and discussion neglect the direct climatic influences from the Pacific Ocean (and records from the west flank of the Andes), particularly ENSO. The authors note in section 195: “Datapoints outside the defined subregions (black dots in Fig. 2a) were excluded from subregional analyses because they were either isolated or located outside subregional definitions, e.g., high

montane sites from NNeo >3000 m; low altitudes from CAn < 2200 m; or positioned on the Andean west flank, which has a distinct climate control relative to the east flank and Altiplano”. The climatic dynamics influenced by the Pacific Ocean cannot be overlooked, particularly given that their effects can be detected globally (e.g. ENSO). If the analyzed records did not exhibit a clear signal, this should be explicitly stated. Similarly, if the sampling resolution is insufficient for the western flank, as has been acknowledged for other regions with limited data coverage such as Northeastern Brazil (NEB), this limitation should also be addressed. In the same line, it is unclear why ecosystems from high mountains, such as paramos, are excluded from the analysis. Several of them have proven useful for understanding past climatic variability (e.g. Haggemans et al., 2022, Espinoza et al., 2022, Ledru et al., 2022). It is worth mentioning that the northern part of the Andes was completely excluded in this study.

Response #3. Thanks for the relevant comment. We will include records from the Northern Andes (i.e., records located north of 0° latitude) down to 24 °S, and use all available sites above 2200 m a.s.l. Therefore, the section currently designated *Central Andes* section will be renamed to *Tropical Andes* to more accurately reflect its broader latitudinal scope. To maintain consistency in terminology, the section previously designated as *Southern Andes* will be renamed *Extratropical Andes*.

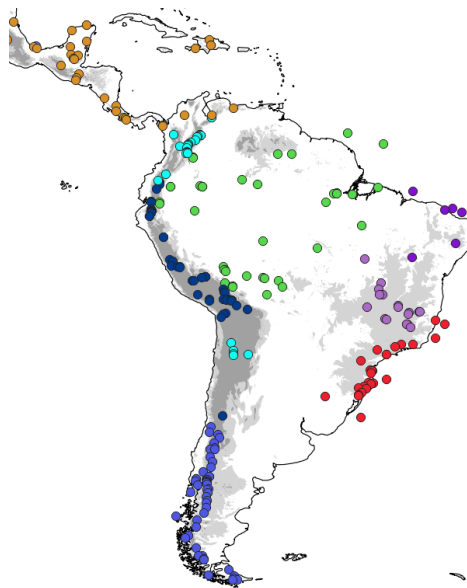


Figure. Cyan dots depict records which will be included in the analysis for the *Tropical Andes* section.

We will also include discussions on potential ENSO impacts. However, given the long-term scope of our study and the broad spatial and temporal coverage of our dataset, it is difficult to assess short-term variability. Moreover, the simultaneous intensification of ENSO during the late Holocene, after a damped mid Holocene phase (Carré et al., 2014; Koutavas et al., 2006; Moy et al., 2002) coincides with

increasing human influence on the landscape and land-use patterns, making it challenging to disentangle their respective effects (e.g., Nascimento et al., 2020). Nevertheless, we will briefly include discussions on how ENSO may have contributed to the observed changes and incorporate the updated ENSO activity curve from Laguna Pallcacocha (Mark et al., 2022) to Fig. 7 from the manuscript (see preliminary version of the updated figure below, Fig. R3.1). Additionally, we will introduce a new figure in the Appendix (Fig. R3.2), which separates the northern and southern Tropical Andes at 8°S. The discussion in the renamed section “5.2.3 Tropical Andes (TrAn)” will be slightly adapted to reflect these changes, as exemplified below.

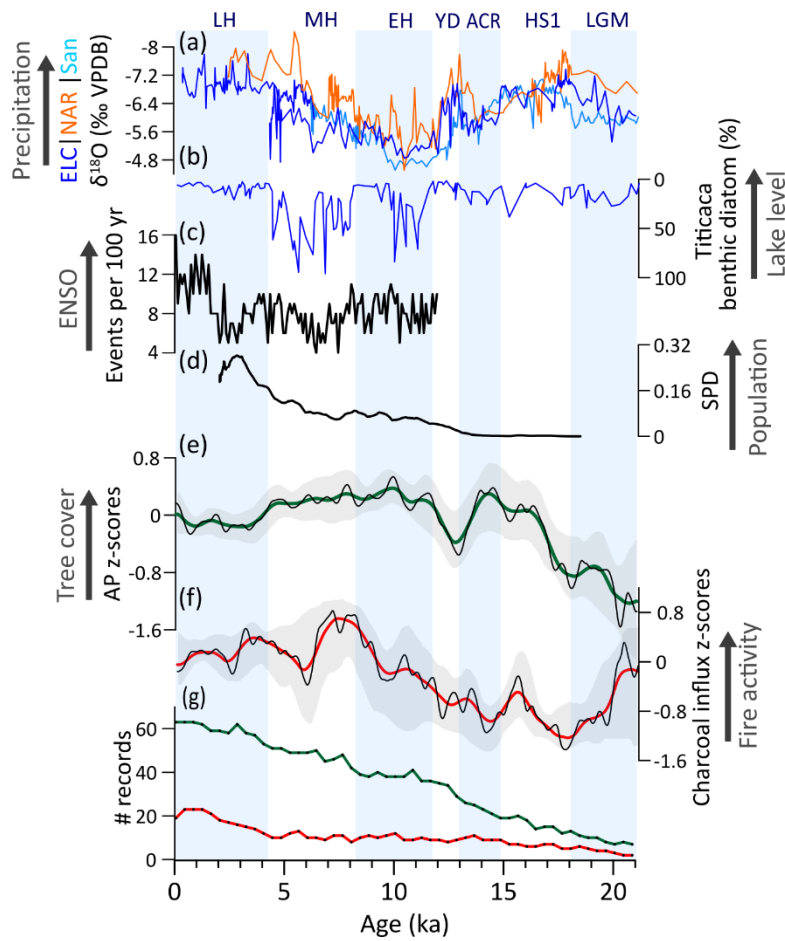


Fig. R3.1 Updated Fig.7. Tropical Andes (TrAn) vegetation, fire, climate regimes, and human populations: (a) Speleothem $\delta^{18}\text{O}$ from El-Condor (ELC), Cueva del Diamante (NAR), and Santiago (San) caves (Cheng et al., 2013; Mosblech et al., 2012). (b) Freshwater benthic diatom (%) from Titicaca Lake (Baker et al., 2001). (c) XRF-based reconstructed ENSO frequency from Laguna Pallcacocha (Mark et al., 2022). (d) Summed density probability of ^{14}C ages from archeological sites in CAN (Goldberg et al., 2016) ($N = 949$). (e) Arboreal pollen (AP) and (f) charcoal influx z-scores composites using 1000-yr (green and red, respectively) and 400 yr (black) smoothing half-window. Gray areas represent 2.5th and 97.5th confidence intervals. (g) Number (#) of records with available pollen (green) and charcoal (red) data in a 400-yr time bin.

5.2.3 Tropical Andes (TrAn) “The MH is characterized by a stepwise intensification of the fire regime, with tree cover remaining relatively stable, as indicated by our regional-integrating AP composite (Fig. 7d,e). However, subdividing TrAn at 8 °S in northern and southern sectors reveals distinct trends (Fig. A3): while fire activity increased across both regions, tree cover remained stable in the north but declines in the south. These trends are consistent with evidence of heterogeneous hydroclimatic patterns along Andes, with drier conditions recorded by lowered lake levels, mainly in the Altiplano region (Baker et al., 2001; Bush and Flenley, 2007; Hillyer et al., 2009) and persistent wet conditions recorded in central sectors of the TrAn (Bustamante and Panizo, 2016; Cheng et al., 2013; Polissar et al., 2013) (Fig. 7a). Modern climate patterns indicate that anomalies in equatorial Pacific SST can produce different regional impacts in precipitation by affecting moisture-laden easterlies and the Bolivian High (Garreaud et al., 2003; Poveda et al., 2020; Vuille, 1999). For instance, reduced ENSO variability has been suggested to decrease moisture balance in parts of the Andes, particularly in the southern TrAn, parts of the northern TrAn and NNeo (Fig. A3; Fig. 7c) (Polissar et al., 2013). Accordingly, we observe an apparent negative correspondence between the zonal Pacific SST gradient anomaly and tree cover trends during the EH and MH in southern TrAn, but no apparent control on northern TrAn (Fig. A3). Furthermore, while $\delta^{18}\text{O}$ in ice and speleothem cores primarily reflect rainy season precipitation (Cheng et al., 2013; Vuille et al., 2003), fluctuations in lake levels are influenced by annual precipitation (Theissen et al., 2008). This may alternatively suggest that despite a gradual increase in summer precipitation throughout the Holocene, the MH featured a decrease in annual precipitation over the Altiplano. Nevertheless, the maintenance of some tree cover may indicate the persistence of moist microclimates (Ledru et al., 2013; Nascimento et al., 2019). These conditions, as well as anthropogenic activities, would have favored a regional intensification of the fire regime and decline in tree cover. By ca. 6 ka, agropastoral systems based on maize agriculture and llama herding became widespread (Nascimento et al., 2020).”

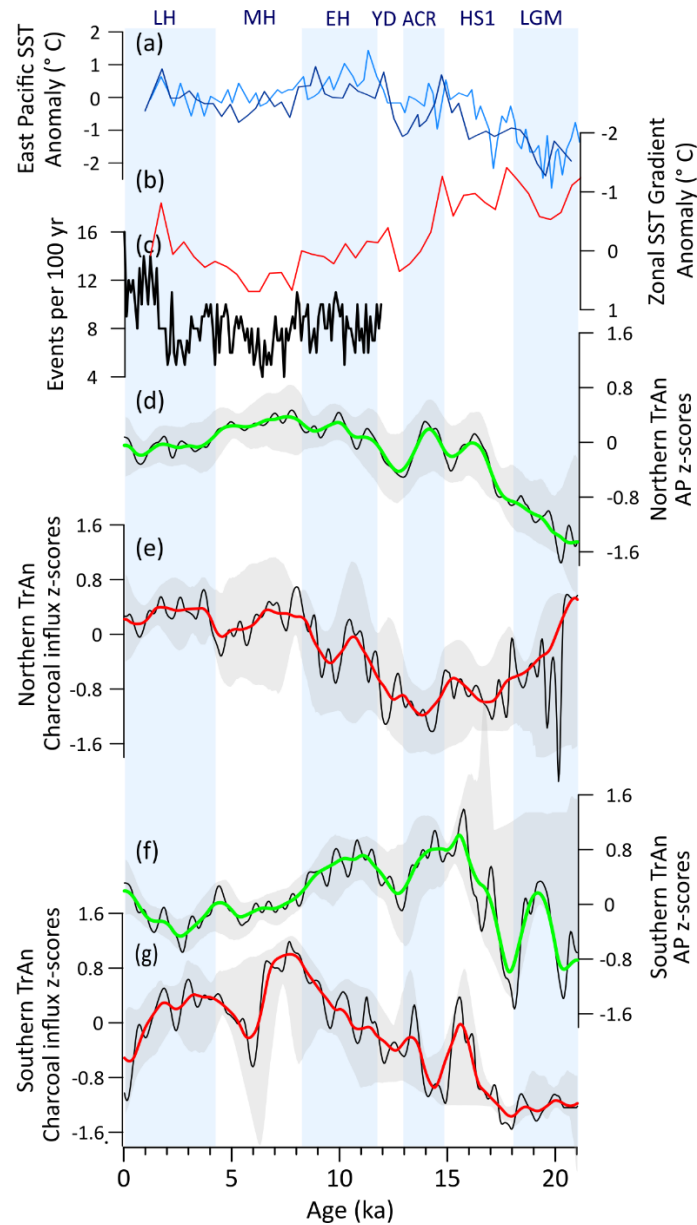


Fig. R3.2. Figure that will be included in the Appendix as Fig. A3 – Tropical Andes (TrAn) subdivided in northern and southern sectors at 8 °S: (a) East Pacific SST anomaly (Koutavas and Joanides, 2012; Lea et al., 2006). (b) Zonal SST gradient anomaly between east and west Pacific (Koutavas and Joanides, 2012). (c) El Niño events per 100 years estimated from XRF data from Lake Pallcacocha (Mark et al., 2022). (d) Arboreal pollen (AP) and (e) charcoal influx z-scores composites from all records from TrAn located north of 8 °S. (f) Arboreal pollen (AP) and (g) charcoal influx z-scores composites from all records from TrAn located south of 8 °S. AP and charcoal-influx z-scores were produced using 1000-yr (green and red, respectively) and 400 yr (black) smoothing half-window. Gray areas represent 2.5th and 97.5th confidence intervals.

References:

- Carré, et al.: Holocene history of ENSO variance and asymmetry in the eastern tropical Pacific, *Science*, 345, 1045–1048, <https://doi.org/10.1126/science.1252220>, 2014.
- Koutavas, et al.: Mid-Holocene El Niño-Southern Oscillation (ENSO) attenuation revealed by individual foraminifera in eastern tropical Pacific sediments, *Geology*, 34, 993–996, <https://doi.org/10.1130/G22810A.1>, 2006.

Koutavas, A. and Joanides, S.: El Niño-Southern Oscillation extrema in the Holocene and Last Glacial Maximum, *Paleoceanography*, 27, 1–15, <https://doi.org/10.1029/2012PA002378>, 2012.

Lea, et al.: Paleoclimate history of Galápagos surface waters over the last 135,000 yr, *Quat. Sci. Rev.*, 25, 1152–1167, <https://doi.org/10.1016/j.quascirev.2005.11.010>, 2006.

Mark, et al.: XRF analysis of Laguna Pallcacocha sediments yields new insights into Holocene El Niño development, *Earth Planet. Sci. Lett.*, 593, 117657, <https://doi.org/10.1016/j.epsl.2022.117657>, 2022.

Moy, et al.: Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch, *Nature*, 420, 162–165, <https://doi.org/10.1038/nature01194>, 2002.

Nascimento, et al.: The adoption of agropastoralism and increased ENSO frequency in the Andes, *Quat. Sci. Rev.*, 243, 106471, <https://doi.org/10.1016/j.quascirev.2020.106471>, 2020.

In the methodology, it is not entirely clear how the authors have standardized the pollen data. It draws my attention to the part where they have “excluded mangrove and aquatic taxa, fern spores and unidentified types”. In the case of fern spores, the authors should evaluate or clarify if they have considered tree ferns in their AP composite. In some regions, such as the Atlantic and Andean Forests, tree ferns, like *Cyathea*, *Lophosoria*, or *Dicksonia* species thrive under specific conditions, with water availability being a common factor. In pollen records, they serve as key indicators of humid conditions and are included in the pollen sum (Kesler et al., 2011, Salazar et al., 2013, de Gasper et al., 2021).

Response #4. We addressed the concern regarding the standardization of the methodology in our Response #2 to Reviewer #2 (Raquel F. Cassino).

Regarding tree ferns, while we recognize their value as indicators of humid conditions in regions such as the Andes and Atlantic Forests, we excluded them from the pollen sum due to inconsistent reporting across records. Including them would have limited comparability among sites. To maintain a standardized dataset suitable for regional-scale analyses, we chose to exclude all fern spores from the pollen sum. We acknowledge that this may compromise some site-specific interpretations, but it improves the overall inter-comparability of the dataset.

The following paragraph will be included in the method section:

“Although tree ferns can serve as important indicators of humid conditions in regions such as the Andes and Atlantic Forests, we excluded them from the pollen sum due to inconsistent reporting across records, in order to ensure a standardized dataset suitable for regional-scale analyses.”

Regarding fire dynamics, it is unclear how the authors determined high or low fire activity. The methodology from the compiled data is not evident. Additionally, the type of data used to reconstruct fire regimes, whether macrocharcoal, microcharcoal, or both is not specified.

Response #5. We use the methodology described in Blarquez et al. (2014). This method has also been used in other compilation studies (Daniau et al., 2012; Marlon et al., 2013; Mooney et al., 2011; Power et al., 2010). The composite z-score curve represents interpolated values using a LOWESS derived from individual site z-scores, which indicate how far charcoal influx at each site deviates from the mean. Positive and negative composite z-scores correspond to periods of above- and below-average charcoal influx, respectively, which we interpret as stronger or weaker fire regimes. While our approach does not allow us to distinguish specific aspects of the fire regime such as intensity, severity, frequency, seasonality, spatial extent of the burned vegetation, we use the broader terms "fire regime" or "fire activity" to reflect the general response of fire to environmental changes, which is directly interpreted from values of charcoal influx. Still, prompted by this comment, we will improve a specific passage of the methods by clarifying this aspect of our interpretations as follows:

“Changes in charcoal records can be linked to past fire activity and used to infer shifts in fire regimes. While our approach does not allow to resolve specific components of the fire regime (e.g., intensity, severity, frequency, seasonality, spatial extent of burned vegetation), we consider fire regime as the collective changes in charcoal influx trends within a given region over long timescales. We use fire activity as a more general term to describe variability in charcoal influx.”

Regarding charcoal descriptions, it was indeed insufficiently explained in the manuscript. Both macroscopic and microscopic charcoal data were treated jointly. We will provide further methodological details about charcoal records (see our Response #3 to Reviewer #1 Nicholas O’Mara).

References:

- Blarquez et al.: Computers & Geosciences paleofire : An R package to analyse sedimentary charcoal records from the Global Charcoal Database to reconstruct past biomass burning, Comput. Geosci., 72, 255–261, <https://doi.org/10.1016/j.cageo.2014.07.020>, 2014.
- Daniau et al.: Predictability of biomass burning in response to climate changes, Global Biogeochem. Cycles, 26, 1–12, <https://doi.org/10.1029/2011GB004249>, 2012.
- Marlon et al.: Global biomass burning: A synthesis and review of Holocene paleofire records and their controls, Quat. Sci. Rev., 65, 5–25, <https://doi.org/10.1016/j.quascirev.2012.11.029>, 2013.
- Mooney et al.: Late Quaternary fire regimes of Australasia, Quat. Sci. Rev., 30, 28–46, <https://doi.org/10.1016/j.quascirev.2010.10.010>, 2011.
- Power et al.: Fire history and the global charcoal database: A new tool for hypothesis testing and data exploration, Palaeogeogr. Palaeoclimatol. Palaeoecol., 291, 52–59, <https://doi.org/10.1016/j.palaeo.2009.09.014>, 2010.

Similarly, the authors should pay careful attention to the interpretation of fire dynamics in ecosystems such as savannas, in which the fuel for fire primarily comes from grasses. The authors used AP to determine the available biomass to be burned;

however, for these types of systems, grasses and herbs should also be considered (Alvarado et al., 2020).

Response #6. Thanks for this comment. We will revise parts of the text to more clearly distinguish between the terms “biomass” and “tree cover”. We agree with the observation, and this is particularly evident for central-eastern Brazil, where fire activity has an opposite pattern to AP. Please, also see our Response #4 to Reviewer #2 (Raquel F. Cassino).

5.2.5 Central-eastern Brazil (CEB) “*In CEB, long-term tree cover changes are negatively correlated with fire activity (Fig. 9b,c, Fig. A1d). This pattern points to a feedback mechanism in which herbaceous vegetation facilitates fire activity, while fire, in turn, contributes to the dominance of herbs by limiting tree encroachment. Conversely, moisture-driven development of woody formations leads to the suppression of fire, which further contributes to tree cover expansion (Fig. 9b,c, Fig. A1d).*”

I hope these suggestions are useful to complement this outstanding review, and I congratulate the authors on their efforts to contribute to the understanding of Neotropical ecosystems at different time scales.

We thank Paula A. Rodríguez-Zorro very much for all observations and comments about our manuscript.

REFERENCES

- Steiger, N.J., Smerdon, J.E., Seager, R. et al. (2021). ENSO-driven coupled megadroughts in North and South America over the last millennium. *Nat. Geosci.* 14, 739–744
- Hagemans et al., (2022). Intensification of ENSO frequency drives forest disturbance in the Andes during the Holocene. *Q. Sci. Rev.* 294, 107762
- Espinoza, I. G., Franco-Gaviria, F., Castañeda, I., Robinson, C., Room, A., Berrío, J. C., et al. (2022). Holocene fires and ecological novelty in the high colombian cordillera oriental. *Front. Ecol. Evol.* 10:895152.
- Ledru, M.-P., Aquino-Alfonso, O., Finsinger, W., Samaniego, P., & Hidalgo, S. (2022). Changes in the vegetation and water cycle of the Ecuadorian páramo during the last 5000 years. *The Holocene*, 32(9), 950-963.
- Kessler, M., Kluge, J., Hemp, A., Ohlemüller, R. (2011). A global comparative analysis of elevational species richness patterns of ferns. *Glob. Ecol. Biogeogr.* 20, 868–880.
- Salazar, L., Homeier, J., Kessler, M., Abrahamczyk, S., Lehnert, M., Krömer, T., & Kluge, J. (2013). Diversity patterns of ferns along elevational gradients in Andean tropical forests. *Plant Ecology & Diversity*, 8(1), 13–24
- De Gasper, A. L., Grittz, G. S., Russi, C. H., Schwartz, C. E., Rodrigues, A. V. (2021). Expected impacts of climate change on tree ferns distribution and diversity patterns in subtropical Atlantic Forest. *Perspect. Ecol. Conserv.* 19, 369–378.
- Alvarado, S. T., Andela, N., Silva, T. S., and Archibald, S. (2020) Thresholds of fire response to moisture and fuel load differ between tropical savannas and grasslands across continents, *Global Ecol. Biogeogr.*, 29, 331–344