



## Commentary

## C<sub>4</sub> plant food loss probably influenced *Paranthropus boisei*'s extinction: A reply to Patterson et al.'s commentary on Quinn and Lepre (2021)

Rhonda L. Quinn<sup>\*</sup>, Christopher J. Lepre

School of Earth, Environment and Society, Bowling Green State University, Bowling Green, OH, 43402, USA

## ARTICLE INFO

## Article history:

Received 22 March 2022

Accepted 15 September 2022

## Keywords:

*Paranthropus boisei*

Mid-Pleistocene Transition

Woody cover

Pedogenic carbonate stable isotopic analysis

East African Rift System

Patterson et al. (in press) provide a commentary on our publication in Scientific Reports, Quinn and Lepre (2021), which documents significant decreases in C<sub>4</sub> grasslands in the northern part of the East African Rift System (EARS) coincident with *Paranthropus boisei*'s extinction and the mid-Pleistocene Transition (MPT, 1.3–0.7 Ma). The MPT is a global climatic event, when Earth's glacial-interglacial terminations change from occurring every ~40 kyr before the MPT but averaged ~100 kyr post-MPT (Raymo et al., 1997, 2006). We proposed that a decrease in the abundance of C<sub>4</sub> grasslands during the MPT interval, influenced by increases in atmospheric carbon dioxide (CO<sub>2</sub>) and monsoonal rainfall, impacted *P. boisei*'s survivorship by reducing its preferred C<sub>4</sub> plant foods and increasing competition among the abundant C<sub>4</sub>-feeders in the EARS.

Patterson et al. (in press) suggest that the stable carbon isotopic record of pedogenic carbonates ( $\delta^{13}\text{C}_{\text{PC}}$ ) used to generate a compiled data set of fraction woody canopy cover ( $f_{\text{WC}}$ , Cerling et al., 2011) in the EARS during the MPT interval is not representative of the known spatial distributions of *P. boisei* but are “a function of elevated  $f_{\text{WC}}$  values at two spatially restricted locations (i.e., Nachukui and Dikika) rather than a regional pattern recorded across all of the available evidence from eastern Africa” (Patterson et al., in press: 1). The authors also contend that even if there was a significant decrease in C<sub>4</sub> vegetation during the MPT in the EARS, it may not have negatively impacted the survivorship of *P. boisei*. Patterson et al. (in press) tested this hy-

pothesis by applying a proxy of  $f_{\text{WC}}$  tolerances in four groups of extant mammals, each sharing particular traits with *P. boisei*.

In this response, we test the Patterson et al.'s (in press) first hypothesis that our compiled EARS  $f_{\text{WC}}$  record does not represent large-scale changes in vegetation during the MPT interval with a new spectral analysis of the Omo-Turkana  $\delta^{13}\text{C}_{\text{PC}}$  record to detect orbital periodicities. We discuss resolution discrepancies in other EARS  $\delta^{13}\text{C}_{\text{PC}}$  records and the spatial extent of the C<sub>3</sub> excursion. In addition, we suggest that the authors' counterargument suggesting that *P. boisei* would have sustained an increase in woody cover suffers from survivorship bias and the use of extant fauna, which are nonanalogous to behavioral ecological preferences of *P. boisei* and other Pleistocene C<sub>4</sub> specialists in the EARS.

### 1. An Omo-Turkana $\delta^{13}\text{C}_{\text{PC}}$ record of paleoclimate

Patterson et al. (in press) conducted an alternate time-series analysis without the Nachukui and Dikika data sets and showed that there was no C<sub>3</sub> excursion during the MPT interval. Indeed, the two highest temporal resolution data sets of the 1.3–0.7 Ma interval, Nachukui and Dikika, contribute more data to the EARS  $f_{\text{WC}}$  compilation during the time of *P. boisei*'s extinction (Quinn and Lepre, 2021, Supplementary Figure S7). We do take umbrage with Patterson et al.'s (in press: 1) statement, “we were unable to independently replicate the  $f_{\text{WC}}$  curves.” In fact, Patterson et al. (in press) did not conduct a time-series analysis using the reported and publicly available  $\delta^{13}\text{C}_{\text{PC}}$  data but instead drew a copy of one of our published  $f_{\text{WC}}$  curves using digital imaging soft-

<sup>\*</sup> Corresponding author.

E-mail address: [rquinn@bgsu.edu](mailto:rquinn@bgsu.edu) (R.L. Quinn).

ware. If they simply contacted the corresponding author, then we would have happily provided our parameters used for all time-series analyses conducted in [Quinn and Lepre \(2021\)](#).

[Figure 1](#) shows each  $f_{WC}$  estimate without error bars ([Cerling et al., 2011](#)) based on reported  $\delta^{13}C_{PC}$  values from the individual locales compared to an exponentially smoothed curve of all data points used in the EARS  $f_{WC}$  compilation. These six different locales vary with respect to temporal sampling evenness throughout the 1.3–0.7 Ma interval. But do [Patterson et al.'s \(in press\)](#) results confirm that  $f_{WC}$  values from Nachukui ([Quinn and Lepre, 2021](#)) and Dikika ([Cerling et al., 2011](#)) are ‘highly localized’ spatial signals and not indicators of regional paleovegetation?

Recent work by the Hominin Sites and Paleolakes Drilling Project (HSPDP; [Campisano et al., 2017](#); [Cohen et al., 2016](#)) demonstrates that vegetation communities from EARS basins were responsive to orbitally forced climate change ([Cohen et al., 2022](#); [Lupien et al., 2022](#)). Regional variations in monsoonal rainfall, generated by the orbital phenomena, impacted vegetation in eastern African hominin habitats. The HSPDP has generated several lacustrine sediment proxy records, which average basin vegetation spatially but offer a high temporal resolution due to high sedimentation rates. In contrast, pedogenic carbonate isotopic records reflect a small spatial extent (~1 m<sup>2</sup>) but form over long periods (~100s–1000s years), integrating  $\delta^{13}C_{PC}$  values of vegetation structure during the time of nodule formation. As reviewed in [Monger et al. \(2009\)](#),  $\delta^{13}C_{PC}$  values vary with landscape scale influences such as hydrological and tectonic regimes, depositional setting, and other basin and sub-basin factors (elevation, temperature, humidity), but also are patterned by controls operating at the biome scale such as regional/global climate and CO<sub>2</sub>. Paleosol isotopic records from individual hominin locales typically do not reach sufficient sample sizes or time depths to conduct spectral analysis for detecting orbital periodicities. Chronological dating resolution and depositional hiatuses in many basins also pose limits to time-series and spectral analyses. However, in comparison, the Omo-Turkana pedogenic carbonate isotopic data compilation is a highly resolved, robustly sampled record that is well constrained in time and integrates isotopic values from three spatially distinct areas (Nachukui, Koobi Fora, and Shungura).

We tested [Patterson et al.'s \(in press\)](#) hypothesis that our compiled data only represent a ‘spatially-limited’ vegetation signal by conducting spectral and statistical analyses of the Omo-Turkana  $\delta^{13}C_{PC}$  data set during the MPT interval to determine if the basin  $\delta^{13}C_{PC}$  record carries multiple indications of astronomical periodicities. We predicted that if the Omo-Turkana  $\delta^{13}C_{PC}$  record represents a ‘highly-localized’ signal during the MPT, orbital periodicities linked to patterns of global climate would not be detected. We analyzed  $\delta^{13}C_{PC}$  values from the Koobi Fora, Nachukui, and Shungura formations dated to 1.54–0.65 Ma to characterize the Omo-Turkana region, the source of our originally collected data ([Quinn and Lepre, 2021](#)) and the most fossiliferous *P. boisei* locale ([Wood and Constantino, 2007](#)). This period constrains the increase of woody cover during the MPT interval (1.3–0.7 Ma) and the peak C<sub>3</sub> excursion circa 1 Ma as reported in [Quinn and Lepre \(2021\)](#). Multitaper method spectral analysis showed that four periodicities achieved conventional AR(1) noise spectrum and confidence levels greater than 90% ([Fig. 2A–F](#)). Three of these periodicities correspond to short eccentricity (~128 kyr), obliquity (~41 kyr), and precession (~19 kyr); the ~60 kyr may be a harmonic ([Fig. 2B](#)). Large oscillatory patterns in the  $\delta^{13}C_{PC}$  timeseries appear to follow the cycle of short eccentricity ([Fig. 2C–F](#)).

Our analysis demonstrates the expected and well-documented responsiveness of vegetation to regional monsoonal rainfall variations that were forced by orbital cyclicity. Thus, the Omo-Turkana  $\delta^{13}C_{PC}$  record during the MPT interval, is not a ‘spatially-restricted’ data set, but rather a recorder of regional and perhaps global climate-forced vegetation change. We maintain that as the high-frequency oscillations in the Omo-Turkana  $\delta^{13}C_{PC}$  values are patterned by orbitally forced cli-

mate, the C<sub>3</sub> excursion as recorded in the Omo-Turkana  $\delta^{13}C_{PC}$  values was also the result of a large-scale climatic event during the MPT interval. As detailed in [Quinn and Lepre \(2021\)](#), elevated CO<sub>2</sub> confined to the MPT interval ([Da et al., 2019](#)) is a likely candidate.

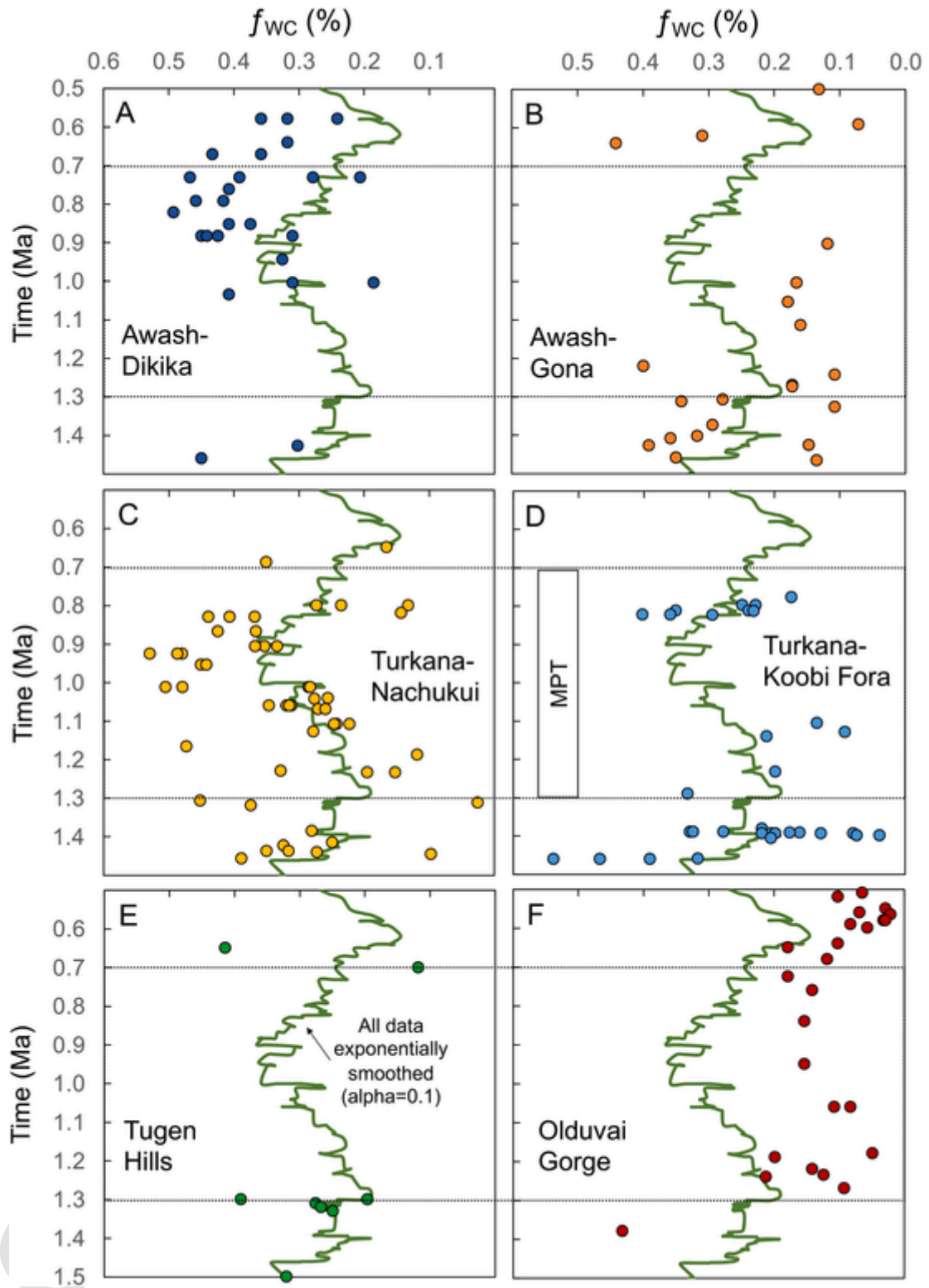
## 2. Paleosol data set resolution discrepancies

Although we disagree with [Patterson et al.'s \(in press\)](#) alternate data treatment, removing Dikika and Nachukui, and reinterpretation of [Quinn and Lepre \(2021\)](#), their commentary makes a good point about resolution discrepancies in various pedogenic carbonate isotopic records, many of which are publicly available in compiled eastern African paleosol isotope databases ([Levin, 2013, 2015](#)). The compilation databases generously made by Levin span nearly 40 years of field and laboratory work by many researchers. With the upmost admiration for the years of painstaking field- and laboratory-based data generation, we note that these data were collected under different experimental conditions depending on the hypothesis(es) tested in each study. Contextual information of each collected sample (e.g., dating, facies analysis, ped structure analysis) and sampling regimes have improved, but in some previous studies, remain undocumented. These associated contextual data are vital for differentiating pedogenic from nonpedogenic carbonates, identifying depositional hiatuses, and for interpreting factors of landscape scale  $\delta^{13}C_{PC}$  differences between basins and subbasins.

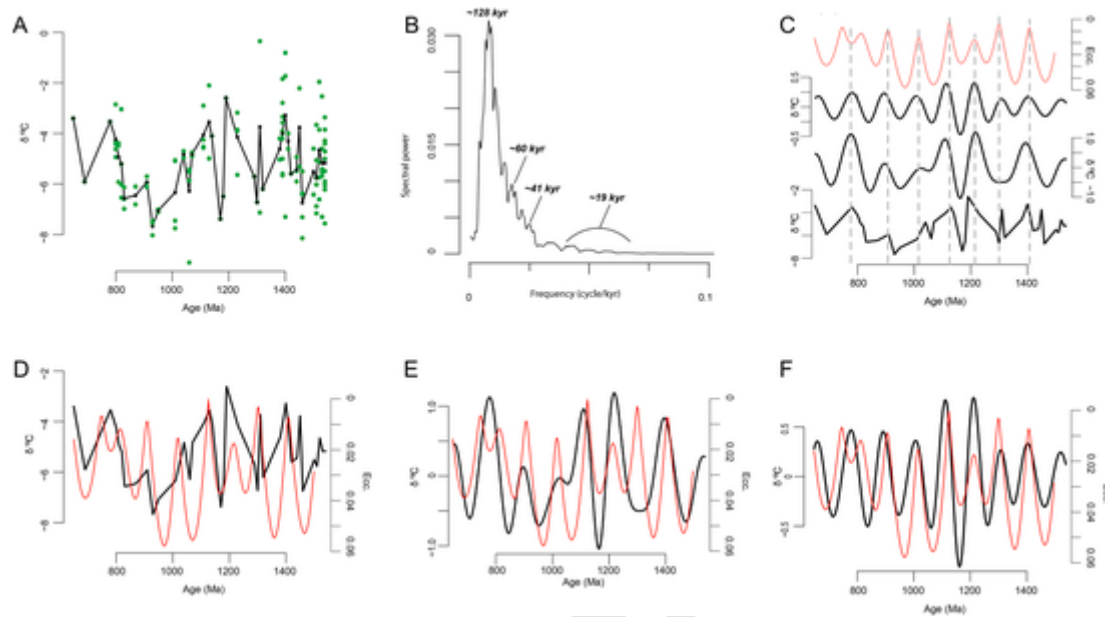
Temporally isolated  $\delta^{13}C_{PC}$  data points from various locales are included in the compiled paleosol databases, but offer no through-time comparisons at that particular locale, and therefore must be treated as potentially idiosyncratic. Isolated isotopic values are problematic for time-series analysis and determining if significant changes in vegetation at that locale occurred since the data sets offer no information up or down stratigraphic section. In [Quinn and Lepre \(2021\)](#), we purposefully excluded  $\delta^{13}C_{PC}$  data from locales that lacked associated sedimentological information and through-time sampling (i.e., multiple samples up/down stratigraphic section) in order to maintain quality of the compiled record from 3 to 0 Ma; these included two 1.3–0.7 Ma interval locales (neither preserve *P. boisei*): Middle Awash (Aduma, 0.9 Ma,  $n = 2$ ; [Yellen et al., 2005](#); Bouri, 1.0 Ma,  $n = 3$ ; [WoldeGabriel et al., 2008](#)) and Ologesailie (1.0 Ma,  $n = 61$ ; [Sikes et al., 1999](#)).

As was the impetus for [Quinn and Lepre \(2021\)](#), several locations that preserve *P. boisei* specimens have little or no available  $\delta^{13}C_{PC}$  data during the estimated time of extinction due to the limited stratigraphic exposure of the 1.3–0.7 Ma interval (e.g., Tugen Hills, Ologesailie), lack of sampling density or study altogether (e.g., Chesowanja, Konso), lack of paleosol preservation (e.g., Malema, Shungura), and/or the presence of unconformities (e.g., Ileret). But an absence of evidence is not evidence of absence. By removing data sets from Nachukui and Dikika, [Patterson et al. \(in press\)](#) interpret that these two locations are responsible for the C<sub>3</sub> excursion and assert that other EARS locales do not show the same pattern. This is not so. As shown in [Figures 1, 3, and 4](#), Ileret and Olduvai Gorge also witnessed reductions in C<sub>4</sub> plants during the MPT interval.

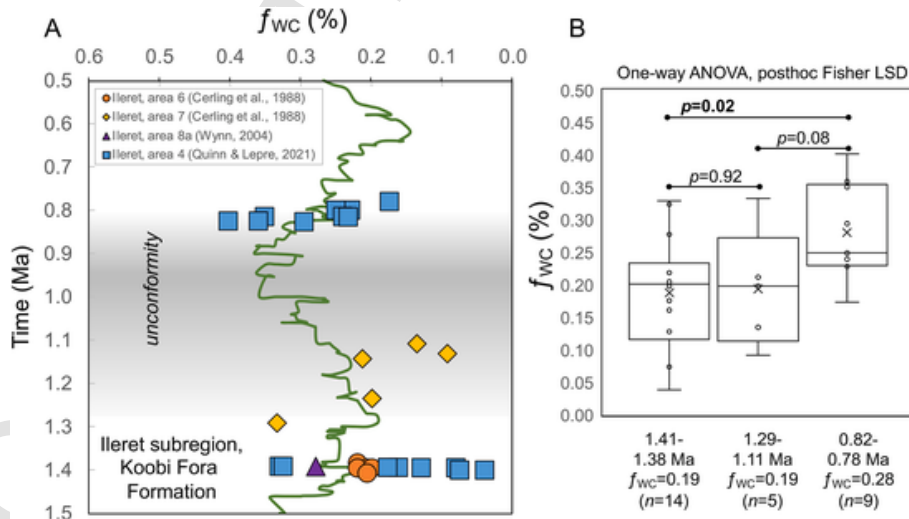
[Patterson et al. \(in press\)](#) state, “... in fact, Quinn and Lepre’s analysis demonstrates that localities to the east (Koobi Fora Formation) and west (Nachukui Formation) of Lake Turkana fail to record the same evidence of a C<sub>3</sub> excursion” ([Patterson et al., in press: 3](#)). This is not a fact. The Ileret locale in the Koobi Fora Formation (east side of Lake Turkana) has a very well-known unconformity that represents ~500 kyr of low/no sediment accumulation through the interval of 1.3–0.7 Ma ([Gathogo and Brown, 2006](#); [McDougall et al., 2012](#)), which, as we reported ([Quinn and Lepre, 2021](#)) significantly limits the characterization of vegetation structure during the MPT interval. Nonetheless, in our original study, we attempted to increase the  $\delta^{13}C_{PC}$  sample size by sampling the paleosols available at Ileret above and below the unconformity. Despite this complication, based on the well constrained and sizable  $\delta^{13}C_{PC}$  sample sets from Ileret ([Fig. 3](#)), average  $f_{WC}$



**Figure 1.** Fraction woody canopy cover ( $f_{wc}$ ) estimates of the East African Rift System locales dated between 1.5 and 0.5 Ma used in compilation of Quinn and Lepre (2021). A) Awash-Dikika, Dikika locale (Busidima Formation) in the Awash Basin of Ethiopia. B) Awash-Gona, Gona locale (Busidima Formation) in the Awash Basin of Ethiopia. C) Turkana-Nachukui, Nachukui Formation (Upper Natoo and Nariokotome members) of the Turkana Basin of Kenya. D) Koobi Fora Formation (Upper Okote and Chari members, Koobi Fora Ridge and Ileret subregions) of the Turkana Basin of Kenya. E) Tugen Hills, Upper Chemeron and Kapthurin formations, Tugen Hills region of Kenya. F) Olduvai Gorge, Upper Bed II, Bed III, Bed IV, and Masek Beds at Olduvai Gorge of Tanzania. The green line on all graphs is an exponentially smoothed curve ( $\alpha = 0.1$ ) of all  $f_{wc}$  estimates based on  $\delta^{13}C_{PC}$  data from these six locales and included in the analysis of Quinn and Lepre (2021). The time interval of the mid-Pleistocene Transition (MPT, 1.3–0.7 Ma) is marked with a dashed-line box across all graphs. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Figure 2.** Spectral and statistical analyses of the Omo-Turkana  $\delta^{13}\text{C}_{\text{PC}}$  data set from 1.54 to 0.65 Ma. A) Raw data from Omo-Turkana are reported in Quinn and Lepre (2021) and Lepre and Quinn (2022). Available open-access at Open Science Framework OSF.IO/J9W2T. Posting-averaging indicates the mean  $\delta^{13}\text{C}_{\text{PC}}$  value of multiple samples collected from a single time datum. B) Multitaper method spectral analysis of the postaveraging time-series interpolated to 1 kyr. Only significant periods that achieved conventional AR(1) noise spectrum and confidence levels greater than 90% confidence are labeled. Periodicities corresponding to short eccentricity (~128 kyr), obliquity (~41 kyr), and precession (~19 kyr) are significant. ~60 kyr may be a harmonic. C) Lowermost curve is postaveraging timeseries as in (A); lower-middle curve is Taner filtering of the postaveraging timeseries using the recommended roll-off rate and high- and low-frequency cutoffs for the last 1 Myr (Zeeden et al., 2018); upper-middle curve is Taner filtering of the postaveraging timeseries using narrower high- and low-frequency cutoffs; uppermost curve is eccentricity solution of Laskar et al. (2004). D-F) are direct comparisons of the three timeseries to the astronomical solution in C. In all three cases, the postaveraging and filtered timeseries recapitulate the eccentricity cycles very well. Note that the eccentricity has been flipped from convention to match the expected relationships with the  $\delta^{13}\text{C}_{\text{PC}}$  (e.g., increased eccentricity = increased monsoonal rainfall and more  $\text{C}_3$  vegetation reflected by less positive  $\delta^{13}\text{C}_{\text{PC}}$  values). Spectral analysis was performed with Astrochron, an R package for astrochronology (Meyers, 2014; Zeeden et al., 2018).

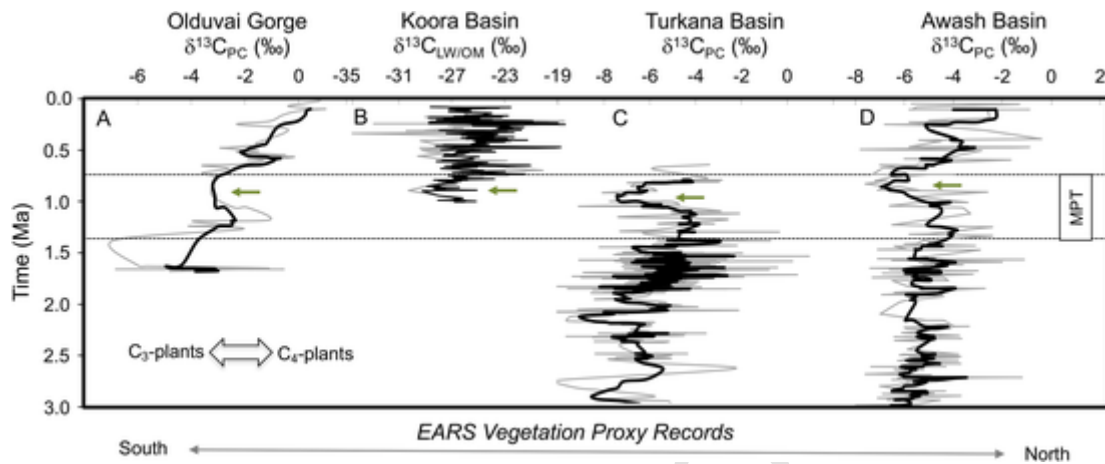


**Figure 3.** A) Fraction woody canopy cover ( $f_{\text{WC}}$ ) estimates of Upper Okote and Chari Members in the Ileret subregion in the Koobi Fora Formation located in the northeastern Turkana Basin, Kenya. B) Box plots of  $f_{\text{WC}}$  estimates separated into three  $f_{\text{WC}}$  time bins (1.41–1.38 Ma, 1.29–1.11 Ma, 0.82–0.78 Ma) and  $p$ -values of one-way analysis of variance and posthoc Fisher least significance difference comparisons.

values significantly increase by 9% (one-way analysis of variance [ANOVA], posthoc Fisher least significant difference,  $p = 0.02$ ) from just before (1.41–1.38 Ma,  $n = 14$ ,  $f_{\text{WC}} = 0.19 \pm 0.09$ ) to the little bit of section above the unconformity (0.82–0.78 Ma,  $n = 9$ ,  $f_{\text{WC}} = 0.28 \pm 0.08$ ). Even with the unconformity, the Ileret  $f_{\text{WC}}$  estimates follow the  $\text{C}_3$  excursion pattern.

Some EARS locales clearly warrant additional paleosol sampling as we suggested in Quinn and Lepre (2021). Olduvai Gorge has preserved paleosols during the MPT interval and was sampled through time

(Cerling and Hay, 1986). Age control is sufficient due to datable and correlative tuffaceous units (Stanistreet et al., 2020). The published Olduvai Gorge  $\delta^{13}\text{C}_{\text{PC}}$  record (Cerling and Hay, 1986) follows the  $\text{C}_3$  excursion (Figs. 1 and 4) but is a very low-resolution data set. We emphasized that Olduvai Gorge is grassier than Omo-Turkana throughout the Pleistocene and maintains the wooded grassland structural category during the MPT interval (Quinn and Lepre, 2021). Observably, EARS basins are variable with respect to temperature (Gebrechorkos et al., 2019), elevation (Junginger and Trauth, 2013), and meteoric water



**Figure 4.** Proxy records of EARS vegetation: basin  $\delta^{13}\text{C}_{\text{PC/OM/LW}}$  values dated to 3–0 Ma, fitted with a 5-point running mean. A) Olduvai Gorge  $\delta^{13}\text{C}_{\text{PC}}$ , B) Koora Basin  $\delta^{13}\text{C}_{\text{OM/LW}}$  (data from Lupien et al., 2021), C) Turkana Basin  $\delta^{13}\text{C}_{\text{PC}}$ , D) Awash Basin  $\delta^{13}\text{C}_{\text{PC}}$  values ( $\delta^{13}\text{C}_{\text{PC}}$  values of B, C–D compiled in Levin 2015; Quinn and Lepre 2021). Dotted-line box denotes MPT interval. Green arrows show reductions in  $\text{C}_4$  plants in four basins with through-time data. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

sources (Levin et al., 2009), which in turn influence vegetation structure and preserved  $\delta^{13}\text{C}_{\text{PC}}$  values (Tieszen, 1991; Sparks and Ehleringer, 1997; Blumenthal et al., 2016). But both locales experienced losses of  $\text{C}_4$  vegetation during the MPT interval (Figs. 1 and 4), as would be expected with a large-scale event. Even though individual locales have different absolute percentages of  $\text{C}_4$  vegetation for *P. boisei* to consume, the overall reduction in  $\text{C}_4$  landscapes within the EARS would have reduced  $\text{C}_4$  plant food availability.

The Awash Basin  $\delta^{13}\text{C}_{\text{PC}}$  record, showing the  $\text{C}_3$  excursion (Quinn and Lepre, 2021), is largely composed of samples from Dikika and Gona. Patterson et al. (in press) remove the Dikika data set to point out that the locale differentially contributed to the  $\text{C}_3$  excursion. Although we understand the point about spatial evenness made by Patterson et al. (in press), we think their exercise reduces temporal resolution, which is critical for a robust time-series analysis. The Dikika samples constitute the majority of samples from the Awash at 1.0–0.7 Ma (Fig. 1), which includes the peak of the  $\text{C}_3$  excursion. By removing the Dikika data set, Patterson et al. (in press) remove data from the MPT interval in the Awash. Compilation  $\delta^{13}\text{C}_{\text{PC}}$  records such as those from the Awash and Turkana (e.g., Cerling et al., 2011) are amalgamations of many locales within basins, which are spatially distributed due to differential preservation. Some fossil and archaeological collecting areas in these basins do not preserve the time interval of study or the materials required for paleoenvironmental reconstructions. Moreover, several different locales must be sampled to generate long proxy records. The long-term increasing trend in  $\text{C}_4$  grasslands commonly shown as a contributing factor of mammalian evolution (e.g., Faith et al., 2018) was compiled with data from several different locales within and across EARS basins. Removing data based solely on its locale is arbitrary, and creating a large temporal gap is problematic for time-series analysis.

### 3. The spatial extent of the EARS $\text{C}_3$ excursion

As reviewed in Trauth et al. (2021), the Onset of Northern Hemispheric Glaciation (ONHG) and glacial intensifications were originally credited as primary drivers of Plio-Pleistocene human evolutionary events (e.g., deMenocal, 1995, 2004; Vrba et al., 1995; Potts and Faith, 2015; Faith et al., 2019), but mounting evidence points to insolation-dominated climatic forcing as the main control on fluctuations in hydroclimate and vegetation structure relevant to biotic evolution in the EARS (e.g., Trauth et al., 2005, 2007, 2009, 2021; Lupien et al., 2018, 2021, 2022; Cohen et al., 2022; Lepre and Quinn 2022). The MPT interval is coincident with a period of higher rainfall during a 405-kyr maximum (Trauth et al., 2005, 2021; Lepre and Quinn 2022) as well as an

increase in  $\text{CO}_2$  (Da et al., 2019), both of which are predicted to promote woody thickening and a reduction in  $\text{C}_4$  plants (Ehleringer et al., 1997; Bond et al., 2003; Bragg et al., 2013).

As we stated in Quinn and Lepre (2021: 6), “our analysis of individual basins demonstrates that the  $\text{C}_3$  excursion occurred in the northern EARS and may not have been a significant event in the central EARS.” Our tentative conclusion was largely due to the low sample density from Olduvai Gorge in the central EARS and the abundance of data from Turkana and Awash from the northern EARS. Moreover, we used  $f_{\text{WC}}$  estimates to gauge changes in the dominant vegetation structural category instead of  $\delta^{13}\text{C}_{\text{PC}}$  values in our time-series analysis, as a means to quantify the magnitude of environmental change with an established calculation and associated structural category definitions (Cerling et al., 2011). Olduvai Gorge’s  $f_{\text{WC}}$  estimates slightly increase during the MPT, but the locale did not change its structural category from wooded grasslands, which was another reason we tentatively concluded a northern EARS event. A 5-point running mean of the individual basin  $\delta^{13}\text{C}_{\text{PC}}$  values shows that Turkana, Awash, and Olduvai Gorge all show excursions to lower  $\delta^{13}\text{C}_{\text{PC}}$  values during the MPT interval (Fig. 4A, C–D). Since our original publication, Lupien et al. (2021) analyzed a continuous leaf wax and organic matter  $\delta^{13}\text{C}$  record spanning the last 1.2 Ma from the Koora Basin in the central EARS and found lower amounts of  $\text{C}_4$  vegetation during the MPT interval compared to after the MPT (Fig. 4B). Finding significant vegetation changes over a ~200–300 kyr interval in high-resolution records spanning distances of 100s–1000 km in the EARS (e.g., Awash, Omo-Turkana, and Koora basins) during a global climatic event corroborates the large spatial scale of the environmental change. That said, we encourage further data collection and hypothesis testing of the  $\text{C}_3$  excursion during the MPT.

### 4. The use of modern analogs versus empirical observations of the past

We respectfully disagree that Patterson et al.’s (in press) model of selected modern mammals informs us about the extinction of *P. boisei*. Although the authors aptly suggest that modern ecological relationships should guide hypothesis generation in paleoecology and paleoanthropology (Faith et al., 2021), we think these particular modern faunal tolerance data have poor explanatory power for the fossil record and specifically for the large-scale evolutionary event during the MPT interval. The major evolutionary event during the MPT interval “represents one of the most significant episodes of faunal change in eastern Africa since the late Miocene” (Faith et al., 2019: 21481). Specifically, non-ruminant grazers abruptly declined at ~1 Ma and were replaced by ru-

minant grazers and mixed feeders, “representing an abrupt reversal of a > 2 Myr-long trend” (Faith et al., 2019: 21481).

Patterson et al. (in press) concluded that selected modern taxa, representing four aspects of *P. boisei*, would survive a ~20% increase in woody cover. Meaning that even if our finding of the C<sub>3</sub> excursion holds, *P. boisei* must have been able to withstand significant losses of C<sub>4</sub> plant foods. The authors also compare modern extant C<sub>4</sub>-grazer speciosity against average rainfall (mm/year) and  $f_{WC}$  values to refute our suggestion that the decrease in C<sub>4</sub> vegetation during the MPT may have heightened dietary competition amongst the abundant C<sub>4</sub>-feeders that had previously evolved in association with C<sub>4</sub> grassland spread. The authors found that extant grazer speciosity peaks between  $f_{WC} = 0.4$ – $0.5$  and concluded that if there was a C<sub>3</sub> excursion during the MPT, the abundant C<sub>4</sub>-feeders, including *P. boisei* would not have experienced heightened competition and reduced survivorship, but would have been able to sustain even larger numbers in habitats that averaged  $f_{WC} = 0.4$ . Notably, the authors' unique approach, analyzing four taxa (three of which are non-primate) that possess different individual adaptive traits yet collectively represent *P. boisei*'s behavioral ecology, was peer-reviewed for the commentary on Quinn and Lepre (2021) but is not yet an established methodology. Recent observations suggest that extant primate taxa are not appropriate analogs of *P. boisei* (Spoonheimer et al., in press). Moreover, Faith et al. (2019) have characterized Plio-Pleistocene hominin ecosystems as nonanalogous to modern faunal communities, which seems at odds with Patterson et al.'s (in press) use of extant mammals in protected wildlife areas to model the ecological tolerance of *P. boisei*.

Patterson et al. (in press) also suggest that the continued presence of C<sub>4</sub> plants in various structural categories including woodlands across the EARS was still ample to feed *P. boisei* populations. One issue here may be underpinned by our use of  $f_{WC}$  estimates rather than  $\delta^{13}C_{PC}$  values or the relative percentages of C<sub>4</sub> plants to quantify vegetation change. We gauged changes in central tendency of EARS vegetation with time-series analyses of  $f_{WC}$  estimates. Of course, this type of analysis does not capture the variation in vegetation communities present in eastern African ecosystems, and the error for calculating an  $f_{WC}$  estimate is rather large ( $1\sigma = \pm 0.203$ ; Cerling et al., 2011). Our finding of a shift from C<sub>4</sub>-dominated habitats to those dominated by C<sub>3</sub> plants was used to infer an overall reduction in the abundance of C<sub>4</sub> plant foods available to *P. boisei* and other C<sub>4</sub>-feeders. We do not doubt that C<sub>4</sub> plants would have been present in various vegetation communities in the EARS as Patterson et al. (in press) suggest. However, we contend that the MPT was a large-scale event that reduced C<sub>4</sub> plant abundances across a range of vegetation structures in the EARS.

In a seminal work, Wood and Strait (2004) characterized *Paranthropus* as tolerant for a diversity of habitats. Thus *P. boisei* may have been a dietary specialist but a habitat generalist focused on specific C<sub>4</sub> plant resources available across environments with different vegetation structures (Quinn and Lepre, in press). Patterson et al.'s (in press) model estimating habitat tolerance via  $f_{WC}$  breadth, however, does not directly address the issue of C<sub>4</sub> plant food loss and its potential impact on *P. boisei*. Vegetation shifts comparable to that of the 1.3–0.7 Ma C<sub>3</sub>-excursion ( $f_{WC}$  ~20% average change) made significant impacts on the evolution of eastern African fauna. The most obvious example is the evolution of C<sub>4</sub> plants and the associated dietary adaptations of eastern African mammals (Cerling et al., 1997, 2015). Several of the coauthors of Patterson et al. (in press) have demonstrated that eastern African mammals evolved in response to steady and incremental increases in C<sub>4</sub> vegetation from the Miocene to the Pleistocene (Uno et al., 2011, 2016; Faith et al., 2018, 2019). Are there reasons to think that only more, not less, C<sub>4</sub> vegetation was capable of influencing faunal evolution?

A better parallel to the demise of *P. boisei* and other nonruminant C<sub>4</sub>-grazers during the MPT may be the ‘Greening of the Sahara’ during recurring African humid periods (AHPs, Menviel et al., 2021) and associated mammalian population crashes (Hempel et al., 2021). For exam-

ple, it has been well documented that woody cover increased across northern Africa and adjacent environments including the EARS during the mid-Holocene AHP (Larrasoana et al., 2013). Although modern humans may have also played a role in biodiversity declines during the mid-Holocene AHP, grazer and grassland-adapted faunal extinctions “are associated with changes in the availability, productivity, or structure of grassland habitats, suggesting that environmental changes played a decisive role in the losses” (Faith, 2014: 105). If Patterson et al.'s (in press) model using extant taxa in protected wildlife areas cannot predict evolutionary patterns associated with the most recent and significant paleoecosystem change in Africa, then how can we assume that these observations explain the evolutionary processes associated with *P. boisei*'s extinction?

Patterson et al.'s (in press) suggestion that the primary influence of C<sub>4</sub>-grazer speciosity is annual precipitation and the resulting water content of C<sub>4</sub> plants (e.g., Olf et al., 2002) and not significant changes in the abundance of C<sub>4</sub> plant food resources conflicts with the evidence of African fossil assemblages and paleoenvironmental records as detailed earlier. That said, the MPT interval has been shown as a period of relatively higher rainfall in the EARS associated with a long eccentricity (405-kyr cycle) maximum (Trauth et al., 2005; Lepre and Quinn, 2022). Higher rainfall promotes the growth of C<sub>3</sub> vegetation at the expense of C<sub>4</sub> vegetation (Sankaran et al., 2005) and, as Patterson et al. (in press) point out, can also reduce the nutrient content in vegetation (Olf et al., 2002). Higher water content in C<sub>4</sub> plants during the MPT may have decreased plant food quality serving as one of several contributing factors to *P. boisei*'s decreased survivorship during the MPT (Quinn and Lepre, in press).

As Faith (2014: 105) concluded, extant grazers are “more ecologically flexible taxa” than their Pleistocene relatives due to “selective taxonomic winnowing” and “loss of grassland specialists” over the last million years. As a nonruminant C<sub>4</sub> plant feeder (Cerling et al., 2013; Martin et al., 2020; Wynn et al., 2020), we proposed that *P. boisei* would have suffered reduced survivorship like several other nonruminant C<sub>4</sub>-grassland specialists in the EARS due to diminishing C<sub>4</sub> plant food abundances and resulting dietary competition among the many C<sub>4</sub>-feeders during the MPT (Quinn and Lepre, 2021). Notably, our proposed selective pressure, a marked reduction in C<sub>4</sub> plant foods, implicates global climate and CO<sub>2</sub> but contrasts that of Faith et al. (2019), who credited enhanced aridity pulses, inferred by the change in periodicities of glacial-interglacial terminations, to have caused the major evolutionary event. It should be noted that there is no empirical evidence yet documented from eastern African fossil locales during the MPT interval to indicate the presence of aridity pulses as inferred by Faith et al. (2019).

We suggest that Patterson et al. (in press) failed to recognize that their selected modern taxa represent a form of survivorship bias (Wald, 1943). This is exemplified by their choice of using savanna-dwelling primates (i.e., baboons), dietary generalists with extremely flexible omnivory. We have few issues with understanding that the behavioral ecology of this taxon may be able to tolerate a ~20% shift in woody cover. However, its relevancy for providing a counterargument for the extinction influences of *P. boisei*, a C<sub>4</sub> plant specialist, is unfounded (Spoonheimer et al., in press).

## 5. Conclusion

The reality of sedimentary (and fossil) preservation necessitates that many spatial areas and temporal intervals are combined to build long-term compilations (e.g., Fox and Koch, 2004; Levin et al., 2011; Fox et al., 2012; Lüdecke et al., 2016; Cohen et al., 2022). Spatial evenness is a methodological goal when attempting to minimize time-averaging and spatial biases for collecting fossil assemblages, but does not directly translate to the biases for sampling Earth's preserved sedimentary record. We fully agree with Patterson et al.'s (in press) general point

that uneven sampling can skew patterns in compilation records impacting interpretations of through-time trends. Indeed, it was the widespread characterization of the MPT in the EARS as ‘grassy’ and ‘arid’ with very few data points from the MPT interval that inspired our original study. But we disagree with the accusation of “scale-jumping.” Patterson et al. (in press) misrepresent pedogenic carbonate isotopic records as ‘highly localized’ without considering the amount of time represented in each individual nodule, and suggest that the methods do not reveal large-scale vegetation changes. It has been shown that individual locale- and basin-scale (landscape scale) variables influence  $\delta^{13}\text{C}_{\text{PC}}$  values (Quinn et al., 2007, 2013; Levin et al., 2011), but  $\delta^{13}\text{C}_{\text{PC}}$  values are also controlled by regional and global factors (biome scale; e.g., Cerling et al., 1993; Basu et al., 2018; Zhu and Tabor, 2021). When paleosol preservation and sampling permit sufficient densities, paleosol data resolve orbital periodicities (Aziz et al., 2008; Lepre and Quinn, 2022), which attests to the biome scale of  $\delta^{13}\text{C}_{\text{PC}}$  records. Our spectral analysis reported here of the Omo-Turkana  $\delta^{13}\text{C}_{\text{PC}}$  record demonstrates that basin vegetation was responsive to regional monsoonal variations driven by insolation and perhaps global climate change and thus is not mainly controlled by ‘spatially-restricted’ factors. Now that we have demonstrated that the Omo-Turkana paleosol record ( $\delta^{13}\text{C}_{\text{PC}}$ ,  $\delta^{18}\text{O}_{\text{PC}}$ ) reconciles orbital forcing (Lepre and Quinn, 2022, this study) like the recent work by the HSPDP based on several lacustrine records (Cohen et al., 2022), the question is not ‘what is anomalous about these high-resolution records?’ but rather ‘why were other EARS paleosol records not sensitive to global climate change?’ Is it an issue with sampling density, a sedimentary preservation problem, or are some basins buffered from biome scale factors?

High-resolution sampling of paleosols from continuous and well-dated stratigraphic sections with detailed sedimentological information is critical for differentiating landscape scale influences of  $\delta^{13}\text{C}_{\text{PC}}$  values from controls operating at the biome scale (Monger et al., 2009). Although the Nachukui Formation is exposed in several areas along the west side of Lake Turkana as stated by Patterson et al. (in press), our goal was to produce the most highly resolved record to date of vegetation securely dated to 1.3–0.7 Ma, the estimated time of *P. boisei*'s extinction, with a high potential for reflecting biome scale environmental change. In Quinn and Lepre (2021), we chose to sample those particular sites in the Nariokotome Member because of the preservation of several paleosols throughout the section, the presence of dated tuffs for reliable age control, and consistent depositional environments. We gauged the potential for landscape scale influences on the Nachukui  $\delta^{13}\text{C}_{\text{PC}}$  values by sampling a second parallel transect ~1 km away, which produced a comparable pattern (Quinn and Lepre, 2021), reducing the probability of landscape scale controls.

We understand Patterson et al.'s (in press) exercise of removing two highly resolved data sets was designed to point out issues in time-series analyses when sample sizes are not evenly spaced. From our perspective, however, their exercise exposed temporal resolution discrepancies in various paleosol data sets rather than limitations with the methodology and our results per se. Certainly, when highly resolved data sets are removed from deep time compilations, observed patterns can change. Patterson et al.'s (in press) commentary also revealed that perhaps our use of  $f_{\text{WC}}$  estimates in Quinn and Lepre (2021) may have obscured the main point for some readers, that significant losses of  $\text{C}_4$  plant foods across the EARS probably influenced the extinction of *P. boisei*.

#### Uncited references

Cerling, 1984, Cerling, 1992, Cerling et al., 1988, Wynn, 2004.

#### Acknowledgments

We appreciate the commentary of Patterson et al. (in press), which generated an interesting exchange of ideas and inspired us to conduct

additional analyses of data from Omo-Turkana. We thank three anonymous reviewers for insightful, thorough, and helpful comments on a previous version of this response.

#### References

- Aziz, H.A., Hilgen, F.J., van Luijk, G.M., Sluijs, A., Kraus, M.J., Pares, J.M., Gingerich, P.D., 2008. Astronomical climate control on paleosol stacking patterns in the upper Paleocene–lower Eocene Willwood Formation, Bighorn Basin, Wyoming. *Geology* 36, 531.
- Basu, S., Sanyal, P., Sahoo, K., Chauhan, N., Sarkar, A., Juyal, N., 2018. Variation in monsoonal rainfall sources (Arabian Sea and Bay of Bengal) during the late Quaternary: Implications for regional vegetation and fluvial systems. *Palaeoogeogr. Palaeoclimatol. Palaeoecol.* 491, 77–91.
- Blumenthal, S.A., Rothman, J.M., Chritz, K.L., Cerling, T.E., 2016. Stable isotopic variation in tropical forest plants and applications in primatology. *Am. J. Primatol.* 78, 1041–1054.
- Bond, W.J., Midgley, G.F., Woodward, F.I., 2003. The importance of low atmospheric  $\text{CO}_2$  and fire in promoting the spread of grasslands and savannas. *Global Change Biol.* 9, 973–982.
- Bragg, F.J., Prentice, I.C., Harrison, S.P., Eglinton, G., Foster, P.N., Rommerskirchen, F., Rullkötter, J., 2013. Stable isotope and modeling evidence for  $\text{CO}_2$  as a driver of glacial interglacial vegetation shifts in southern Africa. *Biogeosciences* 10, 2001–2010.
- Campisano, C.J., Cohen, A.S., Arrowsmith, J.R., Asrat, A., Behrensmeyer, A.K., Brown, E.T., Deino, A.L., Deocampo, D.M., Feibel, C.S., Kingston, J.D., Lamb, H.F., Lowenstein, T.K., Noren, A., Olago, D.O., Owen, R.B., Pelletier, J.D., Potts, R., Reed, K.E., Renaut, R.W., Russell, J.M., Russell, J.L., Schabitz, F., Stone, J.R., Trauth, M.H., Wynn, J.G., 2017. The Hominin Sites and Paleolakes Drilling Project: High-resolution paleoclimate records from the East African rift system and their implications for understanding the environmental context of hominin evolution. *PaleoAnthropology* 2017, 1–43.
- Cerling, T.E., 1984. The stable isotopic composition of modern soil carbonate and its relationship to climate. *Earth Planet Sci. Lett.* 71, 229–240.
- Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeoogeogr. Palaeoclimatol. Palaeoecol.* 97, 241–247.
- Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., Harris, J.M., Hart, J.A., Kirera, F.M., Kaleme, P., Leakey, L.N., Leakey, M.G., Levin, N.E., Manthi, F.K., Passey, B.H., Uno, K.T., 2015. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. *Proc. Natl. Acad. Sci. USA* 112, 11467–11472.
- Cerling, T.E., Bowman, J.R., O'Neil, J.R., 1988. An isotopic study of a fluvial lacustrine sequence: The Plio-Pleistocene Koobi Fora sequence, East Africa. *Palaeoogeogr. Palaeoclimatol. Palaeoecol.* 63, 335–356.
- Cerling, T.E., Hay, R.L., 1986. An isotopic study of paleosol carbonates from Olduvai Gorge. *Quat. Res.* 25, 63–78.
- Cerling, T.E., Wang, Y., Quade, J., 1993. Expansion of  $\text{C}_4$  ecosystems as an indicator of global ecological change in the late Miocene. *Nature* 361, 344–345.
- Cerling, T.E., Wynn, J.G., Andanje, S.A., Bird, M.I., Korir, D.K., Levin, N.E., Mace, W., Macharia, A.N., Quade, J., Remien, C.H., 2011. Woody cover and hominin environments in the past 6 million years. *Nature* 476, 51–56.
- Cohen, A., Campisano, C., Arrowsmith, R., Asrat, A., Behrensmeyer, A.K., Deino, A., Feibel, C., Hill, A., Johnson, R., Kingston, J., Lamb, H., Lowenstein, T., Noren, A., Olago, D., Owen, R.B., Potts, R., Reed, K., Renaut, R., Schabitz, F., Tiercelin, J.-J., Trauth, M.H., Wynn, J., Ivory, S., Brady, K., O'Grady, R., Rodysill, J., Githiri, J., Russell, J., Foerster, V., Dommoin, R., Rucina, S., Deocampo, D., Russell, J., Billingsley, A., Beck, C., Dorenbek, G., Dullo, L., Feary, D., Garello, D., Gromig, R., Johnson, T., Junginger, A., Karanja, M., Kimburi, E., Mbutia, A., McNulty, E., Muiruri, V., Nambiro, E., Negash, E.W., Njagi, D., Wilson, J.N., Rabideaux, N., Raub, T., Seir, M.J., Smith, P., Urban, J., Warren, M., Yadeta, M., Yost, C., Zinaye, B., 2016. The Hominin Sites and Paleolakes Drilling Project: Inferring the environmental context of human evolution from eastern African rift lake deposits. *Sci. Drill.* 21, 1–16.
- Cohen, A.S., Du, A., Rowan, C., Yost, C.L., Billingsley, A.L., Campisano, C.J., Brown, E.T., Deino, A.L., Feibel, C.S., Grant, K., Kingston, J.D., Lupien, R.L., Muiruri, V., Owen, R.B., Reed, K.E., Russell, J., Stockhecke, M., 2022. Plio-Pleistocene environmental variability in Africa and its implications for mammalian evolution. *Proc. Natl. Acad. Sci. USA* 119, e2107393119.
- Da, J., Zhang, Y., Li, G., Meng, X., Ji, J., 2019. Low  $\text{CO}_2$  levels of the entire Pleistocene epoch. *Nat. Commun.* 10, 4342.
- deMenocal, P.B., 1995. Plio-Pleistocene African climate. *Science* 270, 53–59.
- deMenocal, P.B., 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth Planet Sci. Lett.* 220, 3–24.
- Ehleringer, J.R., Cerling, T.E., Helliker, B.R., 1997.  $\text{C}_4$  photosynthesis, atmospheric  $\text{CO}_2$ , and climate. *Oecologia* 112, 285–299.
- Faith, J.T., 2014. Late Pleistocene and Holocene mammal extinctions on continental Africa. *Earth Sci. Rev.* 128, 105–121.
- Faith, J.T., Du, A., Behrensmeyer, A.K., Davies, B., Patterson, D.B., Rowan, J., Wood, B., 2021. Rethinking the ecological drivers of hominin evolution. *Trends Ecol. Evol.* 2855, 1–11.
- Faith, J.T., Rowan, J., Du, A., Koch, P.L., 2018. Plio-Pleistocene decline of African megaherbivores: No evidence for ancient hominin impacts. *Science* 362, 938–941.
- Faith, T.J., Rowan, J., Du, A., 2019. Early hominins evolved within non-analog ecosystems. *Proc. Natl. Acad. Sci. USA* 116, 21478–21483.
- Fox, D.L., Honey, J.G., Martin, R.A., Peláez-Campomanes, P., 2012. Pedogenic carbonate stable isotope record of environmental change during the Neogene in the southern

- Great Plains, southwest Kansas, USA: Oxygen isotopes and paleoclimate during the evolution of C<sub>4</sub>-dominated grasslands. *GSA Bull.* 124, 431–443.
- Fox, D.L., Koch, P.L., 2004. Carbon and oxygen isotopic variability in Neogene paleosol carbonates: Constraints on the evolution of the C<sub>4</sub>-grasslands of the Great Plains, USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 207, 305–329.
- Gathogo, P.N., Brown, F.H., 2006. Stratigraphy of the Koobi Fora Formation (Pliocene and Pleistocene) in the Ileret region of northern Kenya. *J. Afr. Earth Sci.* 45, 369–390.
- Gebrechorkos, S.H., Hultsmann, S., Bernhofer, C., 2019. Long-term trends in rainfall and temperature using high-resolution climate datasets in East Africa. *Sci. Rep.* 9, 11376.
- Hempel, E., Westbury, M.V., Grau, J.H., Trinks, A., Paijmans, J.L.A., Kliver, S., Barlow, A., Mayer, F., Müller, J., Chen, L., Koepfli, K.-P., Hofreiter, M., Bibi, F., 2021. Diversity and paleodiversity of the addax (*Addax nasomaculatus*), a Saharan antelope on the verge of extinction. *Genes* 12, 1236.
- Junginger, A., Trauth, M.H., 2013. Hydrological constraints of paleo-Lake Suguta in the northern Kenya rift during the African humid period (15–5 ka BP). *Global Planet. Change* 111, 174–188.
- Larrasoana, J.C., Roberts, A.P., Rohling, E.J., 2013. Dynamics of Green Sahara periods and their role in hominin evolution. *PLoS One* 8, e76514.
- Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A.C.M., Levrard, B., 2004. A long-term numerical solution for the insolation quantities of the Earth. *Astron. Astrophys.* 428, 261–285.
- Lepre, C.J., Quinn, R.L., 2022. Aridification and orbital forcing of eastern African climate during the Plio-Pleistocene. *Glob. Planet. Change* 208, 103684.
- Levin, N.E., 2013. Compilation of East Africa soil carbonate stable isotope data. *Integrated Earth Data Applications*. <https://doi.org/10.1594/IEDA/100231>.
- Levin, N.E., 2015. Environment and climate of early human evolution. *Annu. Rev. Earth Planet. Sci.* 43, 405–429.
- Levin, N.E., Brown, F.H., Behrensmeier, A.K., Bobe, R., Cerling, T.E., 2011. Paleosol carbonates from the Omo Group: Isotopic records of local and regional environmental change in East Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 307, 75–89.
- Levin, N.E., Zipser, E.J., Cerling, T.E., 2009. Isotopic composition of waters from Ethiopia and Kenya: Insights into moisture sources for eastern African. *J. Geophys. Res.* 114, D23306.
- Lüdecke, T., Schrenk, F., Thiemeier, H., Kullmer, O., Bromage, T.G., Sandrock, O., Fiebig, J., Mulch, A., 2016. Persistent C3 vegetation accompanied Plio-Pleistocene hominin evolution in the Malawi Rift (Chiwondo Beds, Malawi). *J. Hum. Evol.* 90, 163–175.
- Lupien, R.L., Russell, J.M., Feibel, C., Beck, C., Castañeda, I., Deino, A., Cohen, A., 2018. A leaf wax biomarker record of early Pleistocene hydroclimate from West Turkana, Kenya. *Quat. Sci. Rev.* 186, 225–235.
- Lupien, R.L., Russell, J.M., Pearson, E.J., Castañeda, I.S., Asrat, A., Foerster, V., Lamb, H.F., Roberts, H.M., Schäbitz, F., Trauth, M.H., Beck, C.C., Feibel, C.S., Cohen, A.S., 2022. Orbital controls on eastern African hydroclimate in the Pleistocene. *Sci. Rep.* 12, 3170.
- Lupien, R.L., Russell, J.M., Subramanian, A., Kinyanjui, R., Beverly, E.J., Uno, K.T., deMenocal, P., Dommmain, R., Potts, R., 2021. Eastern African environmental variation and its role in the evolution and cultural change of *Homo* over the last 1 million years. *J. Hum. Evol.* 157, 103028.
- Martin, J.E., Tacail, T., Braga, J., Cerling, T.E., Balter, V., 2020. Calcium isotopic ecology of Turkana Basin hominins. *Nat. Commun.* 11, 3587.
- McDougall, I., Brown, F.H., Vasconcelos, P.M., Cohen, B.E., Thiede, D.S., Buchanan, M.J., 2012. New single crystal <sup>40</sup>Ar/<sup>39</sup>Ar ages improve time scale for deposition of the Omo Group, Omo-Turkana Basin, East Africa. *J. Geol. Soc. Lond.* 169, 213–226.
- Menviel, L., Govin, A., Avenas, A., Meissner, K.J., Grant, K.M., Tzedakis, P.C., 2021. Drivers of the evolution and amplitude of African Humid Periods. *Commun. Earth Environ.* 2, 237.
- Monger, H.C., Cole, D.R., Buck, B.J., Gallegos, R.A., 2009. Scale and the isotopic record of C<sub>4</sub> plants in pedogenic carbonate: From the biome to the rhizosphere. *Ecology* 90, 1498–1511.
- Olf, H., Ritchie, M.E., Prins, H.H.T., 2002. Global environmental controls of diversity in large herbivores. *Nature* 415, 901–904.
- Patterson, D.B., Du, A., Faith, J.T., Rowan, J., Uno, K., Behrensmeier, A.K., Braun, D.R., Wood, B.A., 2022. Did vegetation change drive the extinction of *Paranthropus boisei*? *J. Hum. Evol.* <https://doi.org/10.1016/j.jhevol.2022.103154>. In press.
- Potts, R., Faith, J.T., 2015. Alternating high and low climate variability: The context of natural selection and speciation in Plio-Pleistocene hominin evolution. *J. Hum. Evol.* 87, 5–20.
- Quinn, R.L., Lepre, C.J., 2021. Contracting eastern African C<sub>4</sub> grasslands during the extinction of *Paranthropus boisei*. *Sci. Rep.* 11, 7164.
- Quinn, R.L., Lepre, C.J., In press. Environmental and ecological influences of *Paranthropus boisei*'s disappearance from the fossil record. In: Constantino, P., Reed, K., Wood, B. (Eds.), *Paranthropus: The Forgotten Lineage*. Springer.
- Quinn, R.L., Lepre, C.J., Feibel, C.S., Wright, J.D., Mortlock, R.A., Harmand, S., Brugal, J.P., Roche, H., 2013. Pedogenic carbonate stable isotopic evidence for wooded habitat preference of early Pleistocene tool makers in the Turkana Basin. *J. Hum. Evol.* 65, 65–78.
- Quinn, R.L., Lepre, C.J., Wright, J.D., Feibel, C.S., 2007. Paleogeographic variations of pedogenic carbonate  $\delta^{13}\text{C}$  values from Koobi Fora, Kenya: Implications for floral compositions of Plio-Pleistocene hominin environments. *J. Hum. Evol.* 53, 560–573.
- Raymo, M.E., Lisiecki, L.E., Nisancioglu, K.H., 2006. Plio-Pleistocene ice volume, Antarctic climate, and the global  $\delta^{18}\text{O}$  record. *Science* 313, 492–495.
- Raymo, M.E., Oppo, D.W., Curry, W., 1997. The mid-Pleistocene climate transition: A deep sea carbon isotopic perspective. *Paleoceanography* 12, 546–559.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., et al., 2005. Determinants of woody cover in African savannas. *Nature* 438, 846–849.
- Sparks, J.P., Ehleringer, J.R., 1997. Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects. *Oecologia* 109, 362–367.
- Sikes, N.E., Potts, R., Behrensmeier, A.K., 1999. Early Pleistocene habitat in Member 1 Ologesaillie based on paleosol stable isotopes. *J. Hum. Evol.* 37, 721–746.
- Sponheimer, M., Daegling, D.J., Ungar, P.S., Bobe, R., Paine, O.C.C., In press. Problems with *Paranthropus*. *Quat. Int.*
- Tieszen, L.L., 1991. Natural variation in the carbon isotope values of plants: Implications for archaeology, ecology, and paleoecology. *J. Archaeol. Sci.* 18, 227–248.
- Trauth, M.H., Asrat, A., Berner, N., Bibi, N., Foerster, V., Grove, M., 2021. Northern Hemisphere Glaciation, African climate and human evolution. *Quat. Sci. Rev.* 268, 107095.
- Trauth, M.H., Larrasoan, J.C., Mudelsee, M., 2009. Trends, rhythms and events in Plio-Pleistocene African climate. *Quat. Sci. Rev.* 28, 399–411.
- Trauth, M.H., Maslin, M.A., Deino, A., Strecker, M.R., 2005. Late Cenozoic moisture history of East Africa. *Science* 309, 2051–2053.
- Trauth, M.H., Maslin, M.A., Deino, A.L., Strecker, M.R., Bergner, A.G.N., Dühnforth, M., 2007. High- and low-latitude forcing of Plio-Pleistocene African climate and human evolution. *J. Hum. Evol.* 53, 475–486.
- Uno, K.T., Cerling, T.E., Harris, J.M., Kunimatsu, Y., Leakey, M.G., Nakatsukasa, M., Nakaya, H., 2011. Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proc. Natl. Acad. Sci. USA* 108, 6509–6514.
- Uno, K.T., Polissar, P.J., Jackson, K.E., deMenocal, P.B., 2016. Neogene biomarker record of vegetation change in eastern Africa. *Proc. Natl. Acad. Sci. USA* 113, 6355–6363.
- Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), 1995. *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, CT.
- Wald, A., 1943. *A Method of Estimating Plane Vulnerability Based on Damage of Survivors*. Columbia University, Statistical Research Group.
- WoldeGabriel, G., Gilbert, W.H., Hart, W.K., Renne, P.R., Ambrose, S.H., 2008. *Geology and Geochronology*. In: Gilbert, W.H., Asfaw, B. (Eds.), *Homo erectus: Pleistocene Evidence from the Middle Awash, Ethiopia*. University of California Press, Berkeley, pp. 13–43.
- Wood, B., Constantino, P., 2007. *Paranthropus boisei*: Fifty years of evidence and analysis. *Yrbk. Phys. Anthropol.* 50, 106–132.
- Wood, B.A., Strait, D., 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *J. Hum. Evol.* 46, 119–162.
- Wynn, J.G., 2004. Influence of Plio-Pleistocene aridification on human evolution: Evidence from paleosols from the Turkana Basin, Kenya. *Am. J. Phys. Anthropol.* 123, 106–118.
- Wynn, J.G., Alemseged, Z., Bobe, R., Grine, F.E., Negash, E.W., Sponheimer, M., 2020. Isotopic evidence for the timing of the dietary shift toward C<sub>4</sub> foods in eastern African *Paranthropus*. *Proc. Natl. Acad. Sci. USA* 117, 21978–21984.
- Yellen, J., Brooks, A., Helgren, D., Tappen, M., Ambrose, S., Bonnefille, R., Feathers, J., Goodfriend, G., Ludwig, K., Renne, P., Stewart, K., 2005. The archaeology of Aduma Middle Stone Age sites in the Awash Valley, Ethiopia. *PaleoAnthropology* 2005, 25–100.
- Zeeden, C., Kaboth, S., Hilgen, F.J., Laskar, J., 2018. Taner filter settings and automatic correlation optimisation for cyclostratigraphic studies. *Comput. Geosci.* 119, 18–28.
- Zhu, L., Tabor, N.J., 2021. Verification of regional-to-global scale environmental factors in paleosol stable carbon isotope ratios through the lower Permian succession of north-central Texas, USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 582, 110646.