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Commentary

Did vegetation change drive the extinction of *Paranthropus boisei*?David B. Patterson^{a, *}, Andrew Du^b, J. Tyler Faith^{c, d}, John Rowan^e, Kevin Uno^f, Anna K. Behrensmeyer^g, David R. Braun^{h, i}, Bernard A. Woodⁱ^a Department of Biology, University of North Georgia, Dahlonega, GA 30597, USA^b Department of Anthropology and Geography, Colorado State University, Fort Collins, CO 80523, USA^c Natural History Museum of Utah, University of Utah, Salt Lake City, UT 84108, USA^d Department of Anthropology, University of Utah, Salt Lake City, UT 84112, USA^e Department of Anthropology, University at Albany, Albany, NY 12222, USA^f Division of Biology and Paleo Environment, Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY 10964, USA^g Department of Paleobiology, National Museum of Natural History, Washington, DC 20013, USA^h Technological Primate Research Group, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 604103, Leipzig, Germanyⁱ Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, DC 20052, USA

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1. Introduction

Early evaluations of the masticatory morphology of *Paranthropus* (e.g., Robinson, 1954) pointed to it being an ecological specialist. This prompted a decades-long series of evolutionary narratives suggesting that a narrow dietary niche prevented *Paranthropus* from successfully responding to environmental change in the Pleistocene (reviewed in Wood and Strait, 2004). In a recent example, Quinn and Lepre (2021) draw from the eastern African carbon isotope record of pedogenic carbonates (i.e., paleosol isotopes) to hypothesize that an increase in mean fraction woody cover (f_{wc}) during the Mid-Pleistocene Transition (MPT; ~1.3–0.7 Ma) influenced the extinction of *Paranthropus boisei*. Enamel stable isotope data from *P. boisei* are consistent with its heavy reliance on C_4 resources (Cerling et al., 2011a). Quinn and Lepre (2021) propose that this made *P. boisei* vulnerable to an abrupt—on geological time scales—increase in mean f_{wc} and decrease in C_4 biomass, which would have in turn increased competition for C_4

resources, decreased *P. boisei* population size, and ultimately resulted in its extinction.

Quinn and Lepre (2021) variably characterize the mean f_{wc} increase as pertaining to the whole Eastern African Rift System (EARS; e.g., their section header, “Causes of the EARS C_3 excursion”; Quinn and Lepre, 2021: 3) as well as to individual depositional basins within the EARS (e.g., “The Awash (Ethiopia) and Turkana (Kenya) basins have the highest $\delta^{13}C_{PC}$ sampling resolutions across the MPT ... and both record significant reductions in C_4 vegetation... Olduvai (Oldupai) Gorge and Tugen Hills, yielding small samples from the MPT interval... show persistent grassy vegetation structures”; Quinn and Lepre, 2021: 2). With respect to the larger scale of the EARS, we show here that the ‘ C_3 excursion’ presented by Quinn and Lepre (2021) is an artifact of an analysis that was overly influenced by data from two localities: Dikika in the Awash and Nachukui in Turkana. Spatially uneven pedogenic carbonate sampling resulted in a data set and an analysis that does not reflect paleovegetation patterns across the currently known geographic range of *P. boisei*. Concerning their basin-scale characterization, we discuss why vegetation change at this scale is insufficient to cause the extinction of a geographically widespread species. At most, a change at this scale might cause a species’ extirpation, but extinction requires vegetation changes across most, if not all, of the localities occupied by the species. Lastly, even if we accept that the C_3 excursion presented by Quinn and Lepre (2021) reflects what was happening across all of the EARS, we show—via an analysis of the distribution of mean f_{wc} tolerated by modern mammals in African ecosystems—that the observed mean f_{wc} increase during the MPT was unlikely to have had a significant influence on the extinction of *P. boisei*.

2. The importance of considering uneven sampling across space

Paranthropus boisei is known from nine fossil-bearing sequences across the EARS (Fig. 1), with its last appearance datum (LAD) being

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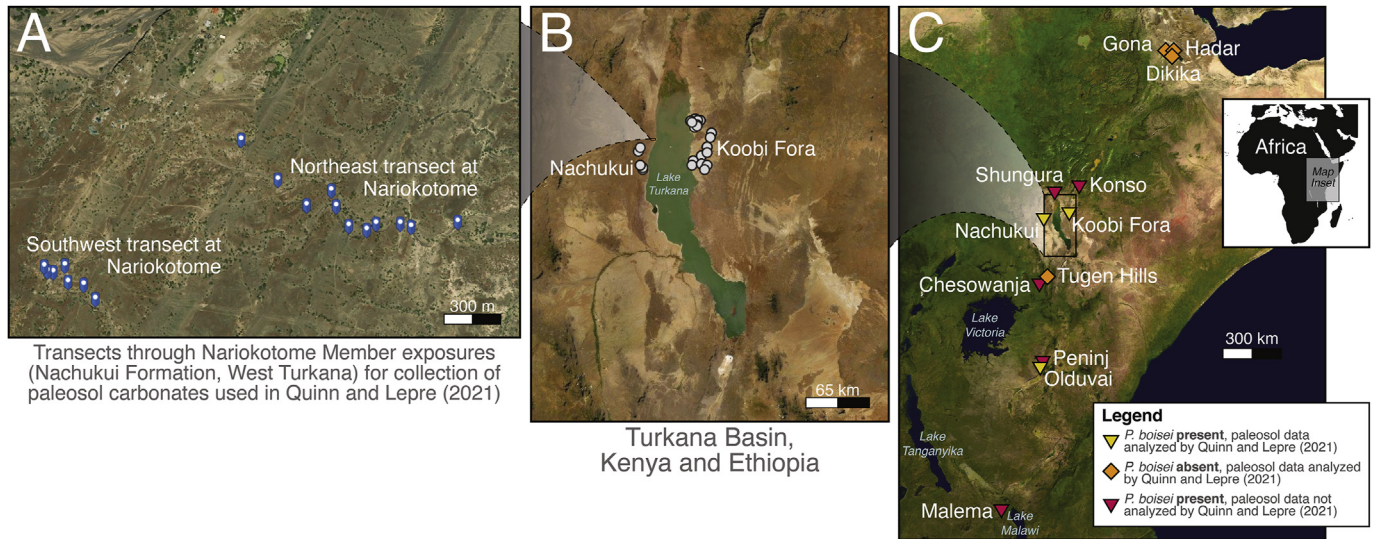


Figure 1. Nested maps showing the spatial scales spanned by paleosol carbonate isotope data and hominin fossil records. A) Paleosol sampling transects across two nearby drainages in Nariokotome Member exposures of West Turkana from Quinn and Lepre (2021: Supplementary Fig. S1). B) The Turkana Basin with points showing the distribution of paleontological localities where specimens of *Paranthropus boisei* have been recovered. C) The distribution of Plio-Pleistocene sites with records of *Paranthropus boisei* (upside-down triangles) or sites with paleosol data from Quinn and Lepre's (2021) regional compilation (diamonds).

1.34 Ma recorded at Olduvai Gorge, Tanzania (Fig. 1; Domínguez-Rodrigo et al., 2013; Wood and Patterson, 2020). As the current LAD is likely older than the actual extinction date of this species because of sampling and taphonomic processes (e.g., Du et al., 2020; Bobe and Wood, 2021), *P. boisei* may well have gone extinct during the MPT (1.3–0.7 Ma). However, this period is one of the most poorly sampled Plio-Pleistocene intervals for paleosol isotopes and mammal fossils in eastern Africa. Quinn and Lepre (2021) contribute important new carbon isotope data ($n = 53$) from the Nachukui (two localities: Nariokotome A and B) and Koobi Fora

formations in northern Kenya, which they convert to f_{wc} estimates (Cerling et al., 2011b) and add to existing f_{wc} data from Dikika, Gona, Koobi Fora, Nachukui, and the Tugen Hills.

Quinn and Lepre (2021) use smoothing algorithms and Bayesian changepoint analysis (see Quinn and Lepre, 2021: Fig. 3) to assess whether their eastern African dataset provides evidence for any shifts in mean f_{wc} during the MPT. A key concern with such an analysis is geographically uneven pedogenic carbonate sampling through time. The carbonate record for the MPT (Fig. 2A) is dominated by data from Dikika ($n = 19$; 20%) and Nachukui ($n = 39$;

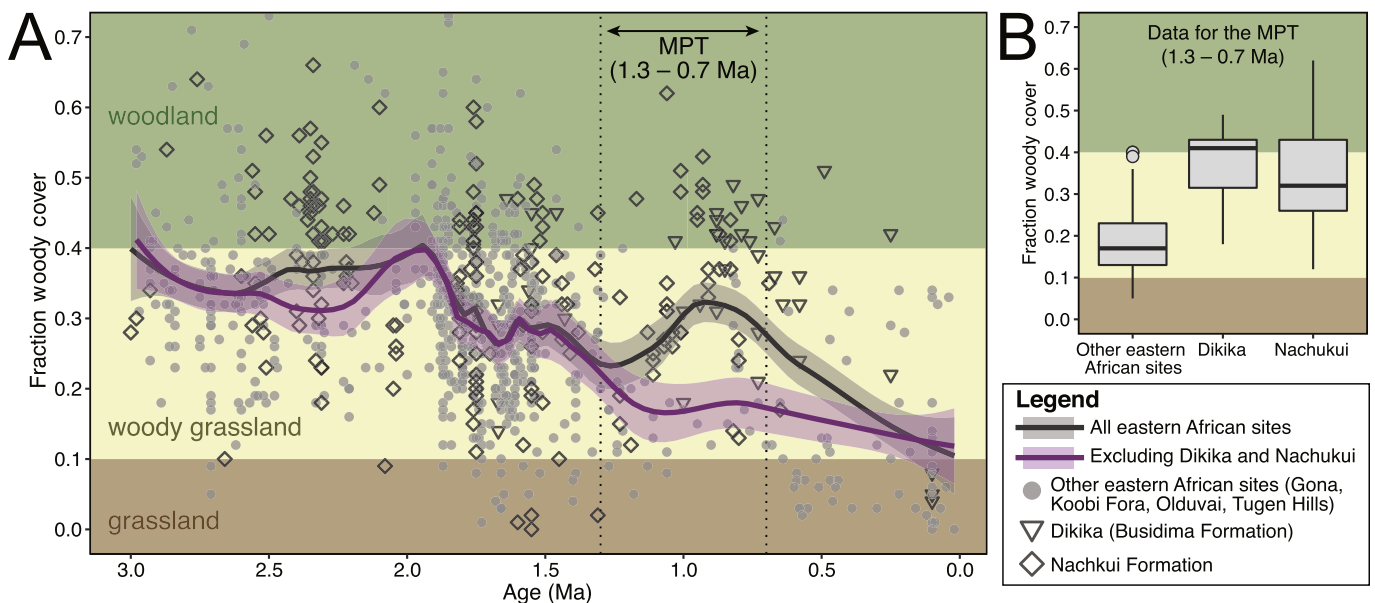


Figure 2. A) Changes in eastern African fraction woody cover over the last 3 Myr, with locally estimated scatterplot smoothing (LOESS) curves (span = 0.2; following Quinn and Lepre, 2021) showing how mean fraction woody cover trends change with the inclusion/exclusion of data from the Busidima Formation at Dikika (upside-down triangles) and Nachukui Formation of West Turkana (diamonds). LOESS curves were drawn using the 'stat_smooth' function in 'ggplot2' v. 3.3.5 (Wickham, 2016) in R v. 4.1 (R Core Team, 2021). B) Boxplot of fraction woody cover values for samples spanning the Mid-Pleistocene Transition (MPT, 1.3–0.7 Ma), showing differences in woody cover at Dikika and Nachukui compared to other eastern African sites. All data from Quinn and Lepre (2021: Supplementary Fig. S3 Dataset).

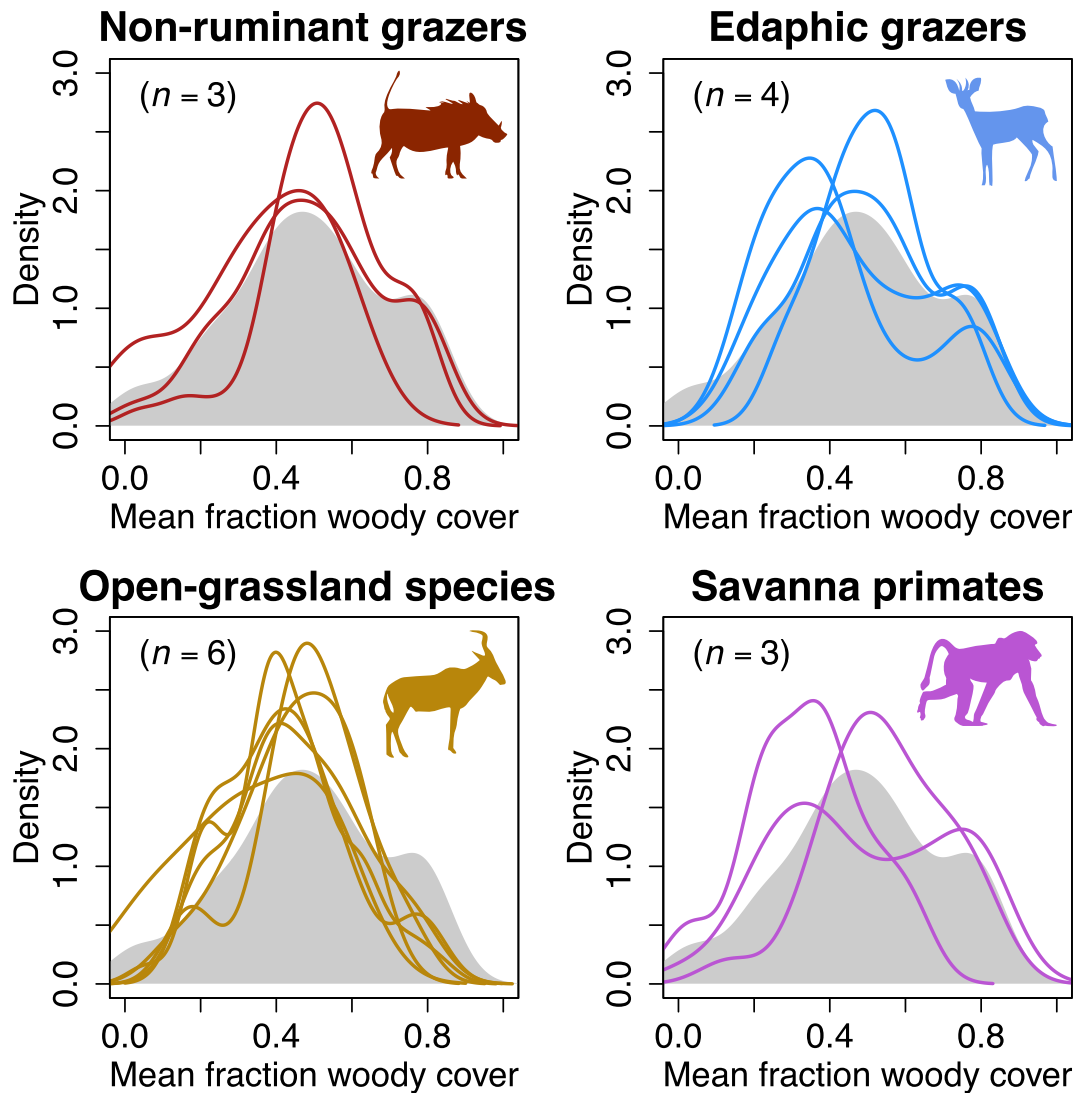


Figure 3. Density plots, wherein each curve (colored lines) depicts the distribution of mean fraction woody cover across all ecosystems occupied by a given species (Table 1; SOM Table S1). Species are organized into four functional groups: nonruminant grazers, edaphic grazers, open-grassland species, and savanna primates. Gray-shaded areas density curves represent the distribution of mean fraction woody cover across all analyzed ecosystems (these are the same in all four panels). All density curves are kernel density estimates, calculated using the ‘density’ function in R v. 4.1 (R Core Team, 2021) with default arguments. Sample size in the top-left of each panel indicates the number of species analyzed within a given functional group. Each analyzed species occupies at least five ecosystems.

41%), both of which are spatially restricted. Although outcrops of the Nachukui Formation are extensive along the west side of Lake Turkana, ~90% of the observations used by Quinn and Lepre (2021) come from just two localities, Nariokotome A and B (Fig. 1A), which collectively span an area of ~1 km² (extent estimated by enclosing sampling points with a minimum convex polygon in ArcGIS Online [Environmental Systems Research Institute, 2021]). The spatial extent of the outcrops from the Busidima Formation at Dikika is larger, but still only a maximum of ~100 km² (Wynn et al., 2008; Campisano et al., 2012; n.b., specific georeferenced point data for the Dikika samples are not available). Dikika and the two Nachukui localities record the highest mean f_{wc} estimates at 0.38 and 0.33, respectively, and are significantly higher (Mann–Whitney U: $p < 0.05$) than contemporaneous values from Gona (mean $f_{wc} = 0.19$; $n = 8$), Koobi Fora (mean $f_{wc} = 0.25$; $n = 14$), Olduvai (mean $f_{wc} = 0.14$; $n = 12$), and Tugen Hills (mean $f_{wc} = 0.24$; $n = 3$; Fig. 2B). The ‘C₃ excursion’ referred to by Quinn and Lepre (2021) is, therefore, a function of elevated f_{wc} estimates at two spatially restricted locations (i.e., Dikika and Nachukui), rather than a regional pattern

recorded across all of the available evidence from eastern Africa (see also Section 3 below). When the Dikika and Nachukui data are excluded, there is no evidence for a mean f_{wc} increase during the MPT (Fig. 2A).

3. Spatiotemporal scale of data vs. spatiotemporal scale of interpretation

Identifying robust connections between paleoenvironmental dynamics and hominin evolution requires aligning the spatiotemporal scale of the research question with that of the available empirical evidence (Faith et al., 2021). The dataset assembled by Quinn and Lepre (2021) indicates that Dikika and Nachukui (specifically Nariokotome A and B) had elevated quantities of C₃ vegetation relative to other locations dating to the MPT (Fig. 2B). Spatial variation in paleovegetation composition across space is well-documented in the eastern African paleosol (Levin et al., 2004, 2011; Quinn et al., 2013) and enamel (Patterson et al., 2017) isotope records. 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 C₃ excursion. Nonetheless, despite previous work by the authors demonstrating such variation (see Quinn et al., 2013), this was not factored into Quinn and Lepre's analysis. Given the data at hand, it would have been instructive to examine why Dikika and Nachukui record higher f_{wc} estimates relative to other locations in eastern Africa during the MPT. Answering this question would not resolve the mystery of why, when, and how *P. boisei* became extinct, but it is interesting as a record of spatial variation in f_{wc} and could help inform future investigations.

Quinn and Lepre (2021) present their work as an investigation of the relationship between vegetation dynamics and the extinction of *P. boisei* across the EARS (Fig. 1C). If the expansion of C₃ environments was the underlying ecological driver of *P. boisei* extinction in the EARS, as they imply throughout their article, demonstrating this convincingly would require that all (or at least a majority) of the localities where *P. boisei* is known record this change in vegetation structure. In other words, the vegetation change should be observed at a spatial scale commensurate with the geographic distribution of *P. boisei* in eastern Africa. Despite this, Quinn and Lepre (2021) only briefly acknowledge differences in vegetation patterns between northern and southern portions of the EARS and interpret the pattern of increased C₃ vegetation at Dikika and Nachukui (i.e., two highly localized, but data-dense sites; Fig. 1), as representative of what was taking place across the entire EARS (see their sections: 'Causes of the EARS C₃ Excursion' and 'A new behavioral and ecological scenario for the extinction of *P. boisei*'). The scale of their inference, therefore, is not matched by the scale of their data.

As noted by Quinn and Lepre (2021), only seven locations (two of which, Middle Awash and Ologesailie, were excluded from their analysis) sample the interval between 1.3 and 0.7 Ma, and of these, only two record elevated mean f_{wc} values (Dikika and Nachukui; Fig. 2) with respect to other values from this interval. Furthermore, even if each of the analyzed pedogenic carbonate samples represents time-averaged vegetation isotope signals spanning 10²–10³ years, they are still hypothesized to represent relatively small portions of the paleolandscape (Du et al., 2019). Based on the above considerations, we conclude that the existing data do not

demonstrate a coeval change in vegetation structure across eastern Africa during the MPT that could be linked to the disappearance of *P. boisei* from this part of the African continent.

4. Relating the observed change in mean f_{wc} to mammalian persistence and extinction risk

Understanding relationships between environmental and evolutionary change requires not only empirical evidence from the geologic and fossil record but also a plausible cause-effect mechanism for transmitting the former to the latter (Behrensmeyer, 2006). Even if we assume that the mean f_{wc} increase during the MPT characterized the whole EARS, is the inferred magnitude of woody cover increase likely to have driven *P. boisei* to extinction? We were unable to independently replicate the f_{wc} curves in Quinn and Lepre (2021: Figure 3) likely because they used a standalone program (Li et al., 2019) and did not specify the exact parameterization of their smoothing algorithms. We therefore used ImageJ v. 1.50i (Schneider et al., 2012) to measure how f_{wc} changed in the exponentially smoothed curve ($\alpha = 0.1$) from Quinn and Lepre (2021: Figure 3A) and found that mean f_{wc} increased from 0.2 to 0.4 during the MPT. To investigate whether such a mean f_{wc} increase would be sufficient to drive *P. boisei* to extinction, we examined the ecological tolerances of modern African mammals with respect to f_{wc} . Specifically, we analyzed for each species the distribution of mean f_{wc} values across its occupied ecosystems to provide an estimate of the range of f_{wc} that the species can tolerate. Following Robinson et al. (2021), we define an ecosystem as comprising one or more protected areas, including national parks and preserves (e.g., Amboseli National Park, Kenya). We included data from across sub-Saharan Africa in our analysis because we were interested in each species' f_{wc} tolerance, a species-level property that would have been incompletely captured if we focused only on one region (e.g., eastern Africa). Only species that occupied at least five ecosystems were included in our analysis. For each of 112 sub-Saharan African ecosystems, we recorded the mean f_{wc} and collected presence/absence data for 16 mammalian species. Mean f_{wc} data are from Barr and Biernat (2020), wherein they calculated for each ecosystem the average across 1 × 1 km f_{wc} pixels from

Table 1

Our 16 analyzed modern species from sub-Saharan Africa, organized into four functional groups: nonruminant grazers, edaphic grazers, open-grassland species, and savanna primates. Each species occupies at least five ecosystems (e.g., Amboseli National Park, Kenya), each of which has one mean fraction woody cover (f_{wc}) estimate. Across each species' mean f_{wc} values, we present the mean, standard deviation, and range. The last column shows each species' probability (p) that an occupied ecosystem has a mean f_{wc} greater than 0.4. This probability was calculated by integrating each species' kernel density estimate from 0.4 to infinity.

	Number of occupied ecosystems	Mean	SD	Range	p (mean $f_{wc} > 0.4$)
Nonruminant grazers					
<i>Equus grevyi</i>	6	0.36	0.20	0.04–0.58	0.478
<i>Equus quagga</i>	62	0.53	0.16	0.04–0.83	0.818
<i>Phacochoerus africanus</i>	102	0.49	0.20	0.02–0.85	0.666
Edaphic grazers					
<i>Kobus ellipsiprymnus</i>	84	0.51	0.18	0.13–0.85	0.697
<i>Kobus kob</i>	30	0.42	0.20	0.20–0.80	0.455
<i>Redunca fulvorifula</i>	18	0.52	0.14	0.29–0.78	0.778
<i>Redunca redunca</i>	55	0.48	0.20	0.13–0.80	0.588
Open-grassland species					
<i>Alcelaphus buselaphus</i>	68	0.46	0.17	0.13–0.83	0.615
<i>Connochaetes taurinus</i>	28	0.48	0.15	0.13–0.78	0.742
<i>Damaliscus lunatus</i>	40	0.43	0.17	0.20–0.80	0.541
<i>Hippotragus equinus</i>	54	0.43	0.16	0.06–0.83	0.555
<i>Nanger granti</i>	16	0.45	0.14	0.13–0.66	0.649
<i>Oryx beisa</i>	9	0.35	0.18	0.04–0.58	0.430
Savanna primates					
<i>Erythrocebus patas</i>	35	0.34	0.16	0.01–0.63	0.360
<i>Papio anubis</i>	59	0.49	0.23	0.01–0.85	0.602
<i>Papio cynocephalus</i>	26	0.55	0.16	0.13–0.83	0.806

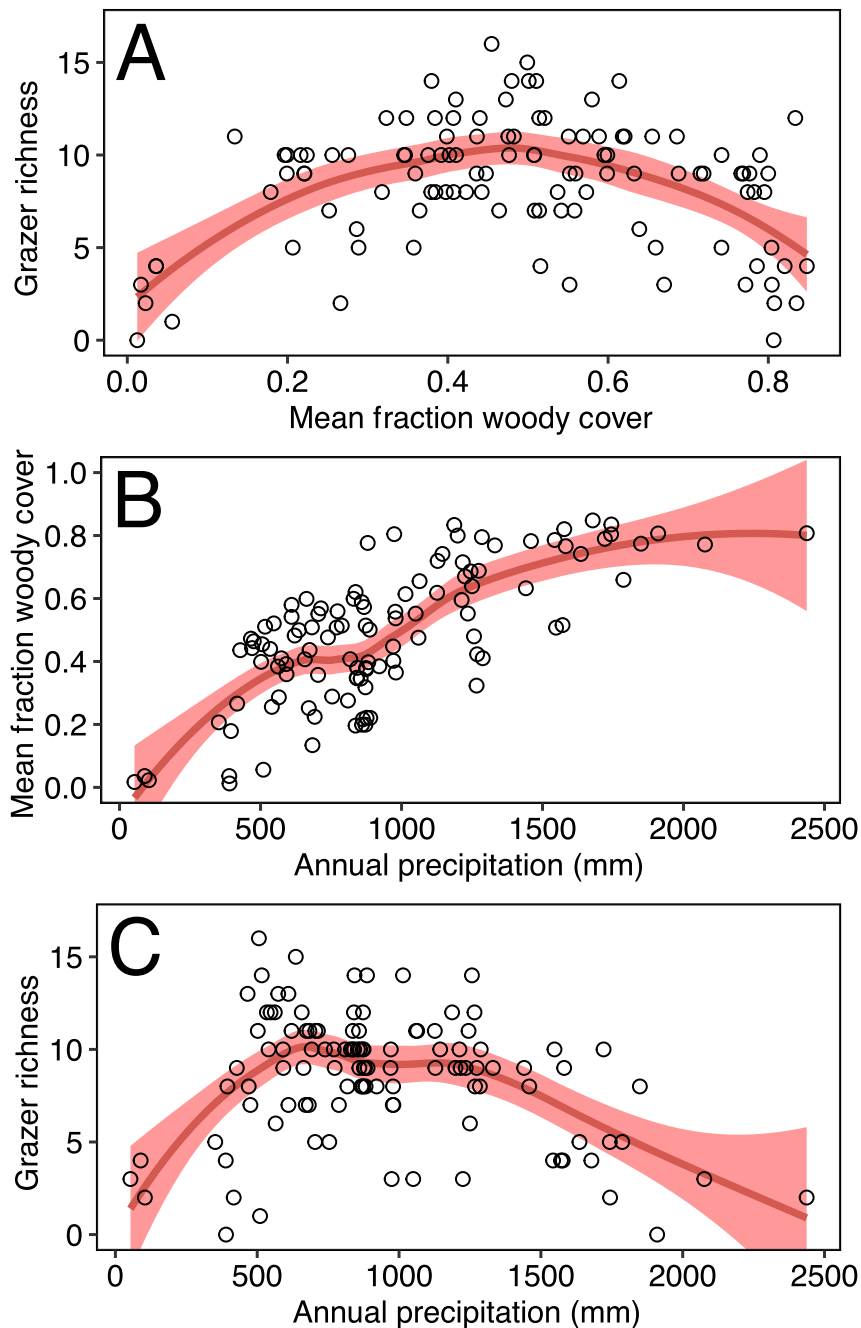


Figure 4. Scatter plots of grazer richness (number of species) as a function of mean fraction woody cover (A); mean fraction woody cover as a function of annual precipitation (in mm; B); grazer richness as a function of annual precipitation (C). Each point is one of 112 analyzed ecosystems, the same that were analyzed in Figure 3. Grazer richness and annual precipitation data are from Rowan et al. (2020) and are included in SOM Table S1. Scatterplot smoothing (LOESS) curves (red lines) were drawn with a smoother span of .75 using the 'stat_smooth' function in 'ggplot2' v. 3.3.5 (Wickham, 2016) in R v. 4.1 (R Core Team, 2021). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

high-resolution satellite imagery (Venter et al., 2018). Mammalian presence/absence data are from Rowan et al. (2020). Our selection of 16 species represents a range of functional traits relevant to understanding the paleoecology of *P. boisei*: (1) nonruminant grazers reflect the digestive physiology and C_4 dietary strategy of *P. boisei* (Cerling et al., 2011a); (2) edaphic grazers, specifically reduncins, are frequently found with *P. boisei* (Shipman and Harris, 1988) and are often associated with sedge-dominated environments, a hypothesized food source for *P. boisei* (Cerling et al., 2011a; Stewart, 2014); (3) open-grassland species, while not necessarily good ecological analogs for *P. boisei*, represent

specialist 'bellwether' taxa. If these species can occupy ecosystems spanning a large range of mean f_{WC} , then this suggests that a C_4 dietary specialist like *P. boisei* could have done the same; and (4) terrestrial savanna-dwelling primates have been proposed as reasonable contemporary models for early hominin dietary and behavioral ecology (Sponheimer et al., 2006; Codron et al., 2008), and presumably like *P. boisei*, these species live in the open savanna and locomote primarily on the ground. Table 1 provides information on our 16 selected species and how they are grouped into the four functional categories (see also Supplementary Online Material [SOM] Table S1 for raw data).

We used kernel density estimation to quantify the distribution of mean f_{WC} values for each species' occupied ecosystems. This was done in R v. 4.1 (R Core Team, 2021), using the 'density' function with default arguments (SOM File S1). It is important to note that such density curves do not describe a species' habitat preference, but should instead be read as indicating a species' ecological tolerance across a gradient of mean f_{WC} values. If a species' density curve does not include certain mean f_{WC} values, this suggests that such values lie outside the species' tolerance. These data serve as a baseline for inferring the magnitude of mean f_{WC} change that is required to increase a species' extinction risk.

Results show that most species' density curves peak around a mean f_{WC} of 0.4–0.5 and extend below 0.2 and far above 0.4 (Table 1; Fig. 3). In fact, it appears that all species occupy ecosystems more or less in proportion to their availability across sub-Saharan Africa with respect to mean f_{WC} (Fig. 3), though this remains to be rigorously demonstrated. Figure 3 shows that all species' density values increase when mean f_{WC} changes from 0.2 to 0.4, indicating that a species' occupied ecosystem is more likely to have a mean f_{WC} of 0.4 compared to 0.2. Indeed, 12 of 16 analyzed species have most of the area under their density curves located above mean $f_{WC} = 0.4$ (Table 1), illustrating that these species are primarily found in ecosystems with a mean f_{WC} greater than 0.4.

Our findings demonstrate that modern mammalian species—with ecologies arguably relevant to understanding the paleoecology of *P. boisei*—can persist in ecosystems with a large range of mean f_{WC} values (Table 1; Fig. 3). Thus, a mean f_{WC} increase from 0.2 to 0.4, as indicated by Quinn and Lepre (2021), is unlikely to drive the species we examined to extinction. In fact, the majority of our selected grassland/grazer species are more likely to be found in ecosystems with mean f_{WC} greater than 0.4, likely because these ecosystems still contain substantial amounts of open habitat dominated by C_4 biomass. These results contradict Quinn and Lepre (2021:1) statement that during the MPT, “The contraction of C_4 grasslands escalated dietary competition amongst the abundant C_4 -feeders, likely influencing *P. boisei*'s demise.” Figure 4a shows that across African ecosystems, there is a hump-shaped relationship between mean f_{WC} and grazer richness (number of species), such that richness actually increases when mean f_{WC} changes from 0.2 to 0.4. Grazer richness is probably not tracking mean f_{WC} per se, but is more likely responding to annual precipitation, which is strongly correlated with mean f_{WC} (Spearman's $\rho = 0.68$; Fig. 4B). Olf et al. (2002) theoretically and empirically showed that herbivore richness peaks at intermediate precipitation values (the same is also true of herbivore biomass; Hempson et al., 2015). This is because too little moisture results in insufficient plant biomass to support large-bodied herbivores that are limited by forage quantity, whereas too much moisture reduces plant nutrient content below the threshold required by smaller-bodied herbivores that are limited by forage quality. Indeed, we find that African grazer richness is highest at intermediate annual precipitation values (Fig. 4C), mirroring the relationship between mean f_{WC} and richness (Fig. 4A). Thus, if the relationship between annual precipitation and mean f_{WC} was the same during the MPT as it is today, an increase in mean f_{WC} from 0.2 to 0.4 would be expected to facilitate greater grazer coexistence and thus increase grazer richness, contra the competition arguments of Quinn and Lepre (2021).

5. Conclusions

Quinn and Lepre (2021) suggest that increasing woody cover between 1.3 and 0.7 Ma (i.e., the MPT) critically influenced the extinction of *P. boisei* in eastern Africa. We argue that this scenario is based on an analysis that is flawed because of uneven sampling in their paleosol dataset. Spatially restricted site samples—Dikika and

Nachukui, both of which have elevated woody cover estimates compared to contemporaneous sites—dominate the data Quinn and Lepre (2021) use to represent this time interval. Yet, Quinn and Lepre use these data to address the question of what caused the extinction of *P. boisei*, a question that requires broader spatial scale data that reflect the distribution of *P. boisei*. We suggest that this is an example of ‘scale-jumping’ that undermines their hypothesized link between environmental cause and effect. It is possible that future work will demonstrate the presence of a C_3 excursion affecting a larger portion of the ecosystems inhabited by *P. boisei* during this interval, and thus provide support for Quinn and Lepre's hypothesis. However, the currently available data are inadequate for this interpretation.

Our analysis of how an ecosystem's mean f_{WC} impacts the persistence of modern African mammals demonstrates that species associated with C_4 environments, including those with diets or digestive physiologies potentially similar to *P. boisei* (i.e., non-ruminant grazers), can tolerate a wide range of mean f_{WC} values. It also demonstrates that an increase in mean f_{WC} from 0.2 to 0.4 can actually promote an elevation in grazer richness, suggesting other limiting factors besides C_4 forage availability. It follows that the localized ‘ C_3 -excursion’ reported by Quinn and Lepre (2021) was probably insufficient to cause the extinction of species associated with C_4 -dominated diets and/or C_4 environments.

Although we welcome the addition of new data from Quinn and Lepre's research, our analysis illustrates the need for caution in proposing links between large-scale environmental causes and hominin evolutionary effects based on proxy evidence for vegetation from limited geographical sampling. This example also underscores the importance of improving our understanding of variation in ecological proxies at local to regional scales, as well as how the observed magnitude of any inferred paleoenvironmental change could have influenced microevolution and macroevolution within the hominin clade.

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Supplementary Online Material

Supplementary Online material related to this article can be found at <https://doi.org/10.1016/j.jhevol.2022.103154>.

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