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Sporadic sampling, not climatic forcing, drives observed early hominin diversity

Simon J. Maxwell\textsuperscript{a,b,1}, Philip J. Hopley\textsuperscript{a,b}, Paul Upchurch\textsuperscript{b}, and Christophe Soligo\textsuperscript{c}

\textsuperscript{a}Department of Earth and Planetary Sciences, Birkbeck, University of London, WC1E 7HX London, United Kingdom; \textsuperscript{b}Department of Earth Sciences, University College London, WC1E 6BT London, United Kingdom; and \textsuperscript{c}Department of Anthropology, University College London, WC1E 6BT London, United Kingdom

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The role of climate change in the origin and diversification of early hominins is hotly debated. Most accounts of early hominin evolution link observed fluctuations in species diversity to directional shifts in climate or periods of intense climatic instability. None of these hypotheses, however, have tested whether observed diversity patterns are distorted by variation in the quality of the hominin fossil record. Here, we present a detailed examination of early hominin diversity dynamics, including both taxic and phylogenetically corrected diversity estimates. Unlike past studies, we compare these estimates to sampling metrics for rock availability (hominin-, primate-, and mammal-bearing formations) and collection effort, to assess the geological and anthropogenic controls on the sampling of the early hominin fossil record. Taxic diversity, primate-bearing formations, and collection effort show strong positive correlations, demonstrating that observed patterns of early hominin taxic diversity can be explained by temporal heterogeneity in fossil sampling rather than genuine evolutionary processes. Peak taxic diversity at 1.9 million years ago (Ma) is a sampling artifact, reflecting merely maximal rock availability and collection effort. In contrast, phylogenetic diversity estimates imply peak diversity at 2.4 Ma and show little relation to sampling metrics. We find that apparent relationships between early hominin diversity and indicators of climatic instability are, in fact, driven largely by variation in suitable rock exposure and collection effort. Our results suggest that significant improvements in the quality of the fossil record are required before the role of climate in hominin evolution can be reliably determined.

Sporadic sampling, not climatic forcing, drives observed early hominin diversity

early hominin diversity | sampling bias | fossil record quality | Africa | climate

The factors that shaped diversification in the hominin lineage have long intrigued paleoanthropologists (1). Much of the debate on the underlying drivers of early hominin diversification has centered on whether change in the hominin fossil record is gradual or pulsed (e.g., refs. 2 and 3), and whether diversification is causally linked to discrete shifts in climate or periods of intense climatic instability (e.g., refs. 4–8). The majority of studies report a direct link between climate and either a taxic diversity estimate (TDE) or the frequency of first appearances (a proxy for speciation) (refs. 9–11, but see ref. 12). In all of these studies, however, fluctuations in TDE are routinely accepted as genuine changes in species richness. This is at odds with a large and growing body of evidence indicating that TDE often largely reflects fluctuations in sampling metrics such as rock outcrop area, fossiliferous formation counts (FFCs), collections counts, and locality counts or their total area, more so than a genuine evolutionary signal (13–22).

The covariation between sampling metrics and paleodiversity can be explained by three hypotheses: (i) the rock record bias hypothesis, that human sampling effort and its underlying driver, rock availability, control observed paleodiversity (13, 15, 23); (ii) the common-cause hypothesis, that both genuine diversity and the rock/fossil records are driven by a third, often environmental, factor (24, 25); or (iii) the redundancy hypothesis, that supposed sampling metrics and the fossil record are redundant with respect to each other (i.e., greater collection effort might result in higher diversity, but higher genuine diversity might also result in more collecting) (26, 27).

Here, we test climatic-forcing hypotheses of early hominin diversification alongside the rock record bias, common-cause, and redundancy hypotheses. To do this, we compared TDE and four phylogenetically corrected diversity estimates (PDEs) (28, 29) to: (i) a strict FFC consisting of only those formations that have yielded a hominin fossil; (ii) a wider FFC consisting of all formations that have yielded a primate fossil; (iii) a comprehensive FFC consisting of all formations that have yielded a terrestrial macromammal fossil; and (iv) a proxy for collection effort: the number of years that have yielded a hominin fossil. Using time series and multivariate analysis, we show that early hominin TDE is greatly affected by temporal heterogeneity in fossil sampling, and that the pattern of diversification frequently linked to discrete climatic events is more apparent than real. Lastly, we demonstrate that each PDE shows little relation to sampling and supports gradual change as the primary mode of diversification in the hominin lineage.

Results and Discussion

Early Hominin Diversity Dynamics. The updated TDE (Fig. 1) is similar to the diversity curve of previous analyses (e.g., ref. 3), displaying three peaks: first, 3.6 million years ago (Ma); second, 2.4 Ma; and third, 1.9 Ma (date refers to the midpoint age of each time bin). Peak TDE ($n = 6$) occurs at 1.9 Ma. These peaks are separated by troughs at 3.0 Ma and 2.0 Ma, and low-standing peaks are driven by a third, often environmental, factor (24, 25); or a common-cause hypothesis, that both genuine diversity and the rock/fossil records are driven by a third, often environmental, factor (24, 25); or the redundancy hypothesis, that supposed sampling metrics and the fossil record are redundant with respect to each other (i.e., greater collection effort might result in higher diversity, but higher genuine diversity might also result in more collecting) (26, 27).

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Is Hominin Diversity Controlled by Sampling? After generalized differencing all time series to remove long-term trends (see Methods and Fig. 1), TDE correlates significantly with both hominin-bearing collections (HBCs) (p = 0.457, P = 0.030) and hominin-bearing formations (HBFs) (p = 0.618, P = 0.002; SI Appendix, Table S2). Both correlations, however, become non-significant after the application of the FDR procedure, and these relationships disappear entirely when HBC and HBF are compared with each PDE (SI Appendix, Table S2). This result could indicate (i) major geological and anthropogenic controls on the sampling of the early hominin fossil record, or (ii) redundancy between early hominin taxic diversity and sampling metrics based solely on counts of early hominin fossils (26, 34). Hominins, like apes today, were probably a minor component of terrestrial ecosystems during their earliest evolution (35) and are therefore expected to be found in a small number of collections/formations during periods of genuine relative low diversity. Conversely, during periods of genuine relative high diversity, hominin fossils are expected to make their way into a greater number of collections/formations. The drive–response relationship between TDE and HBC/HBF is therefore most likely bidirectional, given their interdependence (SI Appendix), and this is corroborated by the fact that the discovery of new hominins and new hominin-bearing formations are intimately linked, having grown in concert through research time (27). However, this non-independence (HBFs are as likely to drive TDE as TDE is HBF) calls into question their usefulness as a meaningful sampling metric (26, 34, 36).

To mitigate the issue of redundancy between TDE and HBFs and more accurately quantify the extent to which sampling controls diversity, we compared TDE to both a wider FCC based on the number of primate-bearing formations (PBFs) and a comprehensive FCC based on the number of terrestrial (i.e., nonmarine) macromammal-bearing formations (MBFs) (SI Appendix, Table S2). Both correlations, however, become non-significant after the application of the FDR procedure, and these relationships disappear entirely when HBC and HBF are compared with each PDE (SI Appendix, Table S2). This result could indicate (i) major geological and anthropogenic controls on the sampling of the early hominin fossil record, or (ii) redundancy between early hominin taxic diversity and sampling metrics based solely on counts of early hominin fossils (26, 34). Hominins, like apes today, were probably a minor component of terrestrial ecosystems during their earliest evolution (35) and are therefore expected to be found in a small number of collections/formations during periods of genuine relative low diversity. Conversely, during periods of genuine relative high diversity, hominin fossils are expected to make their way into a greater number of collections/formations. The drive–response relationship between TDE and HBC/HBF is therefore most likely bidirectional, given their interdependence (SI Appendix), and this is corroborated by the fact that the discovery of new hominins and new hominin-bearing formations are intimately linked, having grown in concert through research time (27). However, this non-independence (HBFs are as likely to drive TDE as TDE is HBF) calls into question their usefulness as a meaningful sampling metric (26, 34, 36).

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unsampled ghost lineages) produces diversity estimates that show little relation to PBF. On the other hand, when MBF is compared with TDE and PDE, no significant correlations emerge (SI Appendix, Table S2).

Because of its combination of layer-cake stratigraphy and exposure of late Miocene to Holocene fossiliferous sediments through rifting and incision, the East African Rift System (EARS) provides a stratigraphically constrained exemplar for understanding the interaction between Neogene climate and mammal diversification (e.g., refs. 37 and 38). When Plio-Pleistocene eastern African (here including Ethiopia, Kenya, and Tanzania) taxic diversity (TDEEA) is analyzed separately, the pervasive nature of sampling is also apparent (see also refs. 37 and 39). Here, TDEEA correlates significantly with both HBEEA (p = 0.546, P = 0.038) and PBEEEA (p = 0.575, P = 0.027) (SI Appendix, Table S3). However, these correlations are rendered nonsignificant after FDR correction. Once again, we find no significant correlation between TDEEA and MBEEA (p = 0.064, P = 0.822).

A highly significant correlation between TDE and PBF on the one hand, and lack of a correlation between TDE and MBF on the other could have three possible explanations: (i) PBF is information redundant with respect to TDE, and MBF (= sampling) does not control diversity; (ii) PBF is information redundant with respect to TDE, and MBF is too broad a measure of the amount of sampling effort in rock suitable for the preservation of a hominin; or (iii) PBF captures a genuine signal of fossil sampling that MBF does not, and largely controls observed TDE. If redundancy were the main cause of these correlations, we would expect the correlation to become weaker the more inclusive the FFC. However, the positive correlation actually increases from HBF to PBF (SI Appendix, Table S2). Further, it is unlikely that TDE drives PBF to the same extent that PBF drives TDE; 39% of PBFs are nonhominin bearing and fossiliferous formations are defined purely on lithostratigraphic grounds. We know of no formations subdivided more finely based on the occurrence of primate fossils, or fluctuations in primate taxic diversity.

For rare and sporadically sampled clades such as hominins, comprehensive FFC might not capture the androsynemic nature of fossil preservation and discovery that wider FFC can (but see the case of pterosaurs; refs. 19 and 26). A lack of correlation between TDE and MBF may be a product of most macro-mammals living in, or being preserved in, habitats that lacked hominins or were unsuitable for them in some way. For example, periods with high MBF could have high TDE if the mammals suitable for preservation in those formations are taphonomically comparable to hominins; but equally, periods with high MBF could have low TDE if the majority of formations preserve habitats unsuitable for hominins, no matter the amount of collection effort a formation receives. This appears to be the case for MBF which, despite containing PBF, correlates weakly with it (p = 0.419, P = 0.048; SI Appendix, Table S2). While cercopithecoid and hominoid primates are taphonomically comparable to hominins in terms of body size, morphology, and habitat preference (40), macro-mammals differ markedly in body size (by several orders of magnitude) and ecomorphology and, as a result, enter the fossil record via different taphonomic pathways. Consequently, the distribution of body sizes in terrestrial mammal assemblages differs markedly by habitat, agent of accumulation, and climate (41). Mammals larger than 180 kg (e.g., Bovidae, Elephantidae, Rhinocerotidae) are overrepresented relative to modern faunas, while the abundance of medium-sized taxa, including large-bodied primates, does not deviate significantly from modern analogs (42). An FFC such as MBF, based on a clade that is preferentially preserved, is therefore less likely to depict a signal of sampling relevant to a rarely preserved and poorly sampled clade.

Defining which formations might preserve a hominin is complex and, to a certain extent, subjective. Although it is better to define a more inclusive clade of interest and compose an FFC based upon its occurrences, the question remains of how wide a clade is required to reach an optimum estimate of sampling intensity (36). Recent model simulations have found that comprehensive FFCs are the best predictor of true sampling, closely followed by all possible formations suitable for the clade of interest and a FFC on a wider clade of interest (36). Our data indicate that a wider FFC based on primate fossils represents the most meaningful count of the number of preserved depositional environments suitable for the preservation of a hominin. FFCs have been argued (e.g., refs. 16 and 34) to be poor predictors of sampling because they do not consistently correlate with collection effort (but see refs. 21 and 24). However, we find a highly significant correlation between PBF and our proxy for human sampling effort both at the continental (p = 0.629, P = 0.002; SI Appendix, Table S4) and regional (p = 0.864, P < 0.001; SI Appendix, Table S3) scales.

These findings are of critical importance for climate-forcing hypotheses of early hominin evolution that interpret global and regional climate events, particularly in the EARS, as causal agents in hominin diversification (e.g., refs. 10–12 and 43). Given the strong relationship between early hominin TDE and sampling found here, purported links between diversification and climate need to be reassessed in a paleobiological framework inclusive of this knowledge.

**Did Climate Drive Hominin Diversification?** Apparent speciation pulses at 3.6, 2.7–2.5, and 1.9 Ma, coincident with step changes in global cooling and African aridification, were first reported in African Bovidae and inferred in early hominins (ref. 4; but see refs. 45 and 45). More recently, these periods have also been argued to correspond with episodes of intense climatic instability in regional dust flux records and the EARS lake variability index (LVI) (e.g., refs. 11, 46, and 47). The timing of these apparent speciation pulses in bovids does, indeed, coincide with peaks in early hominin TDE (Fig. 1). However, peaks in TDE at 3.6, 2.4, and 1.9 Ma map directly onto peaks in both HBC and PBF (Fig. 1), and in the latter case, MBF. In contrast, we find no evidence of pulsed diversification using any PDE (Fig. 1 and SI Appendix, Fig. S1)—diversity estimates that show no significant relation to sampling (SI Appendix, Table S2). Incidentally, peak MBF at 1.9 Ma also coincides with peak diversity of both EARS bovids and Turkana Basin large mammals (37).

To assess whether early hominin diversification dynamics were controlled by climate, we used time series and multivariate analysis to isolate short-term (i.e., bin-to-bin) fluctuations in early hominin TDE and compared this to HBC, PBF, and a record of terrigenous dust flux (henceforth aridity) to the Arabian Sea (5). We repeated the analysis using TDEEA plus a record of West African aridity (48) and LVI (11). This differs from

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**Fig. 2.** Scatter plots showing the relationship between early hominin taxic diversity and possible explanatory variables. A indicates that the time series has undergone generalized differencing before statistical testing. (A) Taxic diversity estimate (TDE) against primate-bearing formations (PBFs). (B) TDE against aridity (5). See SI Appendix, Table S2 for correlation coefficients and P values.
previous research (e.g., refs. 10, 11, 43, and 47) by (i) including metrics for sampling, an aspect of the fossil record hitherto ignored in tests of climate-driven hypotheses of human evolution; and (ii) including an intercept-only null model, equivalent to entirely stochastic evolutionary dynamics, into each analysis. After generalized differencing, we find no link between diversity (either taxic or phylogenetic) and the intercalibrated aridity curve (Figs. 1 and 2 and SI Appendix, Table S2). This indicates that aridity had little effect on short-term fluctuations in early hominin diversity. We also found no link between aridity and any sampling metric, indicating that the observed relationship between TDE and PBF cannot be explained by a common-cause mechanism at the continental scale (at least for the Arabian Sea aridity curve; ref. 5). The common-cause hypothesis proposes that sampling metrics are driven by the same environmental factors that drove paleodiversity. In the case of hominins, a common-cause mechanism could be implied if aridity controlled both the likelihood of a hominin fossil becoming preserved (via changes in the rate of fluviolacustrine sediment deposition) and also diversification rates (i.e., by habitat fragmentation and niche expansion). Such a mechanism could have resulted in a significant but misleading correlation between TDE and PBF, if both were actually independently being driven by a third common cause (24, 25). Despite a causal relationship between aridity and TDE, the complete absence of any correlation between the Arabian Sea and 5-My West African aridity records (48) and LVI (11). Here TDE_BF is best explained by PBF_BF (SI Appendix, Table S5). However, a combination of PBF_BF + Arabian Sea aridity is the second-best model with a difference in \( \Delta r \) of less than 0.001, and a combination of PBF_BF + West African aridity the third-best model. In four of the models with the highest rank, three contain PBF and one HBC. In these models, the only significant predictors are PBF and HBC. The four models with the lowest rank contain aridity as single predictors and in combination, plus a model combining LVI and both aridity proxies. These results indicate that sampling heterogeneity has a considerably greater influence on apparent diversification patterns in the early hominin fossil record than regional climate records. We find no quantitative support for the pulsed turnover hypothesis (4), aridity hypothesis (5), variability selection hypothesis (7, 8), or based on climate-driven pulsed turnover and corroborates recent interpretations that events in human evolution once thought to be major transitions, when viewed in a phylogeographic (i.e., lineage) context, actually represent gradual adaptive shifts (e.g., 3 and 49). The identification of a major sampling component in the early hominin fossil record (SI Appendix, Fig. S2), a sustained and major increase in sampling intensity is undoubtedly required before an accurate understanding of the link between climate and early hominin diversification can be determined.

**Conclusion**

Long-term variation in aridity and climatic instability probably played a key role in the emergent adaptive strategies taken by hominins in the Plio-Pleistocene. However, we find no evidence that short-term fluctuations in climate relate to changes in hominin diversity. Instead, our data support a direct, causal relationship between TDE and fossil sampling. The near-linear increase in PDE from 7.0 to 2.4 Ma negates any explanation based on climate-driven pulsed turnover and corroborates recent interpretations that events in human evolution once thought to be major transitions, when viewed in a phylogeographic (i.e., lineage) context, actually represent gradual adaptive shifts (e.g., 3 and 49). The identification of a major sampling component in the early hominin fossil record indicates that the pattern of diversification which many climatic forcing hypotheses purport to explain is more apparent than real. This should come as no surprise: approximately one-quarter of early hominin species are point occurrences and the remainder have considerable uncertainty in their known stratigraphic durations. Radiometric dating error associated with a first (last) appearance date is not equivalent to statistical uncertainty that the date represents a speciation (extinction) event. Nor is the finding that radiometric dating error is random with respect to a climate event (47) an appropriate test of the quality of the fossil record. If error were
randomly distributed in the early hominin fossil record, any genuine evolutionary signal would be degraded not distorted (50). However, runs tests demonstrate that collection effort ($P = 0.004$) and rock availability ($P < 0.012$ for each FFC) are non-randomly distributed in the early hominin fossil record. The starting point for macroevolutionary analyses in paleoanthropology ought to be that, before any pattern in the fossil record is causally linked to climate, it is demonstrably shown that that pattern is not an artifact of sampling or poor fossil record quality. This requirement has been overlooked by paleoanthropologists, archaeologists, and climatologists alike, and has severely impacted the interpretation of macroevolutionary pattern and process in the early hominin fossil record (51). Becoming cognizant of the rapidly advancing study of fossil record quality in paleobiology, particularly since the pioneering work of Raup (13, 23), should be at the center of 21st century paleoanthropology.

Methods

Taxic Diversity Estimate. Taxic methods assess diversity by counting the number of observed taxa in a series of time bins based on their stratigraphic range. We used the first-appearancedatum (FAD) and last-appearancedatum (LAD) in Wood (52) to calculate the 0.25-My time bins between 7 and 1 Ma (SI Appendix, Table S6). If a FAD or LAD falls on the boundary of a time bin (e.g., 2 Ma), that taxon is deemed present only in the younger bin (in this case, 2–1.75 Ma).

Phylegetic Diversity Estimate. Phylogenetic methods assess diversity by counting the number of lineages (observed and inferred) in a series of time bins using a dated (i.e., time-scaled) phylogeny. We generated PDEs in equivalent time bins using four comprehensive hominin phylogenies (30–33) that sample the largest number of taxa included in the TDE. Polytopies in the strict consensus (30) and majority-rule (32) cladograms were resolved based on the order of first appearance. To maximize comparability between datasets, Eurasian taxa and taxa younger than 1 Ma were pruned from each cladogram after time scaling, as the focus here is early hominin diversification dynamics.

The phylogenetic method requires that branch lengths are proportional to time. To do this we time scaled each tree using taxon duration data and the three-rate-calibrated time-scaling (calc)$^3$ method (53). The calc method constrains the age of each node between the date of the previous node (except for the root) and the FAD of daughter lineages. The age of each node is then calculated by the probability density of the amount of unobserved evolutionary history implied by each node age, a probability dependent on rates of speciation, extinction, and sampling in the fossil record (53). These densities are then used to stochastically sample the possible ages for each node (53). Speciation, extinction, and sampling rates were first determined empirically in the R package paleotree (54). This function applies a maximum likelihood optimization to the distribution of taxon durations and returns the best fitting sampling probability and extinction and speciation rates. The sampling and extinction rates are assumed equal, given the tight relationship observed in the fossil record (56). Results presented for the calculation of speciation, extinction, and sampling rates are based on the taxon durations shown in SI Appendix, Table S6, as the main interest here is the sampling and diversification of early hominin taxa. This method, however, produced an estimated sampling rate that differed markedly from previous estimates for mammals (57). Moreover, the frequency-ratio method (58) did not provide a meaningful estimate of sampling because the frequency distribution of taxon durations violated model assumptions (the equations of ref. 58 require that the frequency distribution of the log of taxon durations is linear). To combat this, the sampling rate reported for primates (0.023 per lineage My; ref. 59) was used plus a maximum root age of 8 Ma. Because node ages are stochastically picked from a distribution defined by the probability of different amounts of unobserved evolutionary history, no single time-scaled tree is correct. Therefore, to account for uncertainty in the age of each node and improve analytical rigor, 1,000 time-scaled trees were generated. The median diversity across all 1,000 trees was calculated along with CIs based on two-tailed 95% upper and lower quantiles (54). It is this median PDE which is used in the statistical tests. Interestingly, the calc method produced median node ages that correlate strongly with the node ages produced by Dembo et al. (31) ($r > 0.98, P < 0.001$) and Dembo et al. (53) ($r > 0.94, P < 0.001$) in their Bayesian tip-dating analyses. Tip-dating methods tend to produce node ages that are several million years older than the minimum (i.e., fossil) divergence date (60), while calc node age distributions tend to be similar to the minimum divergence date (57). The agreement between tip-dating and calc therefore indicates that the range of possible node ages being tightly constrained by the input topologies and FAD.

Sampling Metrics. Rock outcrop. Temporally resolved information on sedimentary rock outcrop area is not available at the continental level for the late Neogene, so instead, we use FFCs. FFCs summarize aspects of rock volume, facies heterogeneity, geographical and temporal dispersion, and collection effort (16, 22) and have been shown to correlate with rock outcrop area (e.g., ref. 21) and gap-bound packages (e.g., ref. 24 but see ref. 61). FFCs represent an estimate of the number of discrete depositional environments known to contain fossils and are thus a proxy for the amount of rock available for sampling in a given time bin. HBF counts were taken from an exhaustive survey of the published literature. Fossil-bearing deposits in the Cradle of Humankind, South Africa, were counted as one “formation” (SI Appendix). This had minimal effect on the results as HBF and a count including each deposit as a distinct formation correlate strongly ($r = 0.941, P < 0.001$). The same treatment is applied to other primate- and mammal-bearing karst deposits. PBF counts were taken from the chapters on cercopithecoids (62), hominins (60), Cenozoic Mammals and Mammalian Faunas in Wood (52) to provide 0.25-My time bins between 7 and 1 Ma (SI Appendix, Table S6). If a PBF or LAD falls on the boundary of a time bin (e.g., 2 Ma), that taxon is deemed present only in the younger bin (in this case, 2–1.75 Ma).

Collecting effort. In-bin counts of the number of HBCs were compiled as a proxy for collecting effort. A collection is defined as an assemblage of fossils from one locality that were amassed in a single effort and is roughly equivalent to a field season. Information on the duration and number of field seasons at a locality are not commonly provided so, instead, we used the number of years that have produced a hominin fossil per formation per bin (SI Appendix). For example, Sahelanthropus tchadensis is known from the 7-Ma and the 8.5-Ma (Chad) and the fossils that compose its hypodigm were collected in 2002 and 2005. The 7.0–6.75 Ma time bin therefore has a HBF count of 2. The number of HBCs in a given time bin thus represents the number of discrete episodes of field study (i.e., paleoanthropological collection effort) that have yielded a hominin fossil. These data are up to date as of November 1, 2017.

Climate proxies. TDE and PDE were compared with the 8-My Arabian Sea (5) and 5-My West African (48) terrigenous dust flux records, and the LVI (11). Dust flux data were interpolated to 50-kiloannum (ka) intervals using the shape-preserving piecewise cubic hermite interpolating polynomial, enabling us to calculate the mean and SD of each time bin. To convert the LVI into our time bins (in the original publication, LVI is given in 50-ka time bins; see figure 1 in ref. 11) we took the mean and maximum value in each time bin.

Statistical Tests. Spearman’s rank (ρ) and Kendall’s tau rank (τ) correlation coefficients were used to compare all diversity estimates, sampling metrics, and climate proxies (66). Time series were detrended and corrected for autocorrelation by generalizing differentiated before regression (ref. 67, R code from www.graemetlloyd.com/methgd.html). Long-term trends and autocorrelation trend to result in spurious detection of correlation between time series (67) and thus must be removed before performing statistical tests (68). The significance of correlations was evaluated based on original $P$ values and $P$ values adjusted for the implementation of multiple tests using the FDR procedure (69). GLS model fitting was performed to explore the possibility of multiple variables explaining taxic diversity, with model fit assessed using the second-order AICc, corrected for finite sample sizes, and the significance of correlations were evaluated based on original $P$ values and $P$ values adjusted for the implementation of multiple tests using the FDR procedure (69). Long-term trends and autocorrelation tend to result in spurious detection of correlation between time series (67) and thus must be removed before performing statistical tests (68). The significance of correlations was evaluated based on original $P$ values and $P$ values adjusted for the implementation of multiple tests using the FDR procedure (69).
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