Plio-Pleistocene African megaherbivore losses associated with community biomass restructuring

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Abstract:

Fossil abundance data can reveal ecological dynamics underpinning taxonomic declines. Using fossil dental metrics, we reconstructed body mass and mass-abundance distributions in Late Miocene to recent African large mammal communities. Despite collection biases, fossil and extant mass-abundance distributions are highly similar, with unimodal distributions likely reflecting savanna environments. Above 45 kg, abundance decreases exponentially with mass, with slopes close to -0.75 as predicted by metabolic scaling. Furthermore, communities prior to ~4 Ma had significantly more large-sized individuals, with a greater proportion of total biomass allocated in larger size categories, than did later communities. Over time, individuals and biomass were redistributed into smaller size categories, reflecting a gradual loss of large-sized individuals from the fossil record, and paralleling the long-term decline of Plio-Pleistocene large mammal diversity.

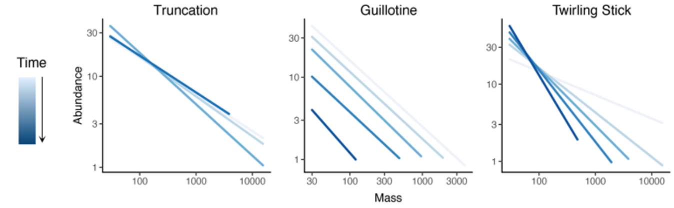
One Sentence Summary: Fossil tooth data show decreases in the abundance and biomass of the largest mammals over the past 4 million years.

Main Text:

Since at least the early 19th Century, the cause of Quaternary megafaunal extinctions has been the subject of much speculation and inquiry (*1*). In particular, a strong case for anthropogenic causes has been made through the coincidence of human arrivals and extinctions in many parts of the world (e.g. *2–5*). In Africa, hominins and large herbivores coexisted for millions of years, and African megafaunal extinctions were initially thought to have been subdued due to coevolution between hominins and their prey (*2*, *3*). However, recent work has shown that the number of large mammal extinctions in Africa did in fact rival that on other continents, and also that megafaunal losses there began far deeper in the past than previously recognized, starting prior to 4 Ma (*6*). Since the earliest records of hominin tool use (and presumably butchery) only go back to 3.3 Ma (*7*), and since evidence for active hunting or increased carnivory during the Early or Middle Pleistocene is lacking (*8*, *9*), the early initiation of megafaunal losses argues strongly against an anthropogenic driver for these extinctions. Environmental scenarios, namely a long-term decrease in CO_2 and the expansion of C_4 grasslands, with resulting losses of large-bodied browsers and mixed feeders, have been proposed as causal factors (*6*, *10*). Additionally, genomic evidence has revealed major population declines during the Middle to Late Pleistocene among many extant large mammal species (*11*), indicating that diversity losses were even greater than previously discerned from the fossil record. Questions remain as to the cause and mechanism of these extinctions and extirpations. One limitation to answering such questions is that studies to date have been largely taxonomically based, tabulating species or genus losses with respect to known climatic or cultural events. In contrast, approaches that tabulate traits at the specimen-level require only minimal taxonomic information, and provide additional analytical sensitivity by incorporating relative abundance data, which permits the examination of ecological dynamics below the species level.

Fossil mass, abundance, and biomass estimates

Here we analyzed changes in the body size structure of late Neogene to recent African large mammal communities using a specimen-based approach. We examined the mass-abundance distributions of individuals in fossil and extant communities and compared it to the relationship, well-established across eukaryotes (*12*), of decreasing abundance per unit area (i.e. density) with increasing body size. In particular, Damuth (*13*, *14*) observed that average population density (N) scales to body mass (M) as $N = M^{-0.75}$, and that, since individual metabolic rates (MR) scale to body mass as $MR = M^{0.75}$, the energy consumed by a population ($E = N \, x \, MR$) is independent of its body mass (i.e. $E = M^{0}$, also termed 'energetic equivalence'). In turn, the biomass (B) of a population is $B = N \, x \, M$, which equates to $B = M^{0.25}$ This 'metabolic scaling' rule explains why larger species within a single trophic level have exponentially lower population densities in comparison with smaller ones, and also why larger species can pack more biomass for each unit of energy extracted from the preceding trophic level (fig. S1). Metabolic scaling therefore predicts that, within a single trophic level or taxonomic scale, abundance should scale to mass raised to an exponent of -0.75, and biomass to mass raised to an exponent of 0.25 (*15*).



Description	Decreasing abundance then loss of largest individuals	Decreasing abundance of all sizes with loss of largest individuals first	Decreasing abundance of larger individuals, increasing abundance of smaller individuals
Possible Cause	Hunting of large individuals	Decrease in primary productivity	Vegetation change causing larger sizes to be relatively less efficient at converting energy to biomass
Expectations	Increasingly negative slope returning to initial value after loss of targeted size category	Constant slope with decreasing y-intercept (if absolute abundance can be measured)	Decreasing slope values

Fig. 1. Three scenarios describing changes in mass-abundance distributions as a result of megaherbivore losses due to different causes. Abundance can be measured as either relative or absolute for Truncation and Twirling Stick models, but must be absolute to observe a decreasing y-intercept in the Guillotine model. The Twirling Stick is the only model that predicts a long-term change in slope.

Despite extensive examination in ecology, mass-abundance relationships have not been widely investigated in the fossil record. We asked whether the fossil record of African large mammals follows predictions of metabolic scaling, and whether changes in mass-abundance distributions have occurred over time mirroring the long-term decline of megaherbivore diversity (*6*). Specifically, we used fossil community mass-abundance distributions to test among three competing scenarios of megafaunal loss and community structure alteration (Fig. 1). 1: Under a scenario of human hunters targeting the largest species (‘downsizing’), the relationship between mass and abundance becomes more negative as the proportion of large individuals decreases, then rebounds back to its original value when the targeted mass category is extirpated. The result is a community that displays the same mass-abundance slope, but a distribution of body size that is truncated at the larger end (Truncation model, Fig. 1A). 2: Under a scenario of decreasing resources, the total biomass of a community decreases, affecting all sizes equally. Larger species, already less abundant, will be the first to disappear as the carrying capacity shrinks, particularly as their decreasing population densities render them more and more vulnerable to stochastic processes and extinction vortexes (*16*) (Guillotine model, Fig. 1B). The result is a community with an unchanged mass-abundance slope, but decreased total abundance and a loss of the largest individuals. 3: Under a third scenario, the quality and/or distribution of resources shift in a way that disrupts the ability of larger individuals to extract energy and provides a competitive advantage to smaller individuals. Biomass is then redistributed towards smaller size categories and mass-abundance slopes become more negative over time reflecting progressively decreasing abundance, and eventual extinction, of larger size categories (Twirling Stick model, Fig. 1C). These scenarios are obviously not exhaustive, but they do address three common causal hypotheses (anthropogenic downsizing, productivity loss, resource reallocation).

To test among these scenarios we used specimen and metric data from a new compilation of mammalian dental metrics (*17*). Selecting premolars and molars of extant and fossil Artiodactyla, Perissodactyla, Proboscidea, and Primates, we used the relationship between tooth length and average species mass in extant species (*18*) to estimate body mass for fossil specimens and reconstruct the mass-abundance and mass-biomass distributions of extant and fossil communities (figs. S2-S4). Our final fossil dataset consisted of 7430 specimens from 61 communities mainly covering Africa but including data from the Arabian subcontinent as well (table S2). Abundance data for 39 extant communities came from Hatton et al. (*12*), which mainly covers Africa, but includes a few Indian and South American communities (table S3). These are largely from savanna habitats (e.g. grasslands, shrublands, and woodlands), with a small number of tropical forest habitats as well. Additionally, a compilation of 39 African communities based on census data was made for this study (table S4). Sensitivity analyses were also conducted to assess the robustness of our results to different mass estimation approaches and to varying data selection criteria (*19*).

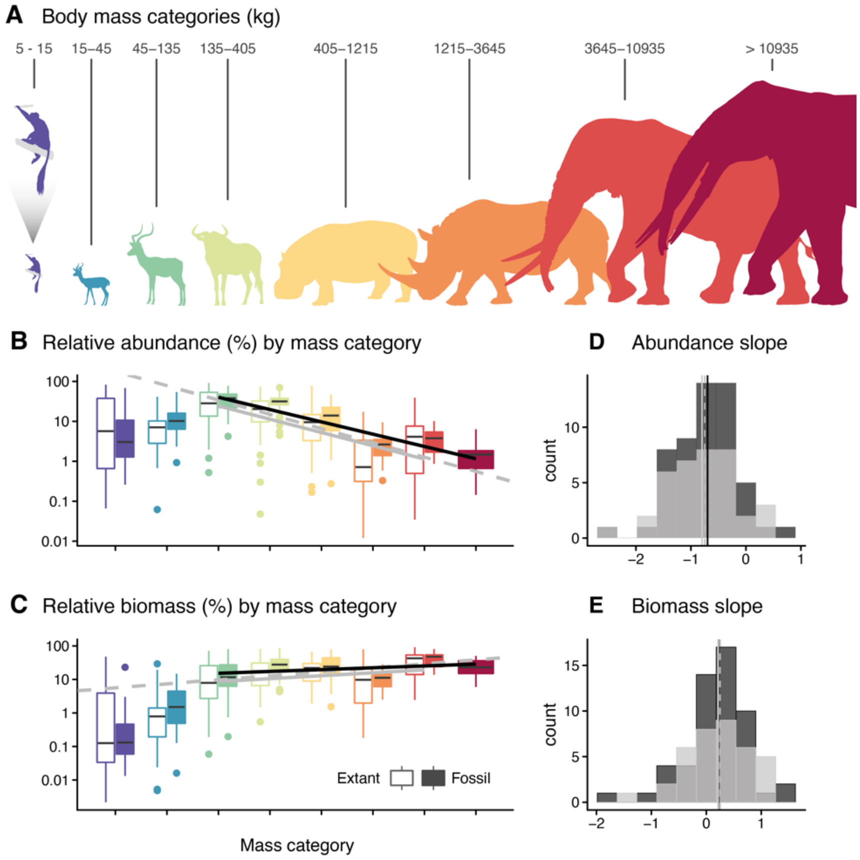


Fig. 2. Individual mass-abundance and mass-biomass distributions in fossil and extant large mammal communities are similar. (**A**), body mass categories with representative taxa to scale (the monkey is enlarged for clarity). In both fossil and extant communities, mass-abundance (**B**) and mass-biomass (**C**) distributions have fewer individuals < 45 kg than predicted by metabolic scaling (dashed grey lines, slopes of -0.75 and 0.25, respectively, *y*-intercept is arbitrary). The greater variance of the 5-15 kg category in the extant data is due to the inclusion of forest communities. Above 45 kg, distributions follow predictions of metabolic scaling (solid lines). Note that *y* axes in **B** and **C** are log-scaled. **D-E**, distribution of mass-abundance (**D**) and mass-biomass (**E**) slopes in fossil and extant communities (>45kg) are similar, with median values (solid vertical lines) close to expectations of metabolic scaling (dashed vertical lines).

Changing abundance and biomass structure since 4 Ma

First, we found that mass-abundance distributions in the African fossil record are similar to those of extant communities (Fig. 2 and figs. S5-S8). Our results indicate that similar fundamental processes underlie mass-abundance relationships in both extant and past communities, and that these are detectable in the fossil record despite taphonomic, collection, and publication biases. A similar finding was recently demonstrated for species abundances in zoological museum collections (*20*). In comparison with extant communities, however, fossil communities include a greater proportion of large individuals, and occasionally individuals estimated to weigh over 10 tons (the largest African elephants today weigh around six tons) (Fig. 2A and fig. S7). Sensitivity tests using different mass estimation approaches and various subsets of the data gave similar results (figs. S10-S15) (*19*).

Second, extant and fossil large herbivore communities are far less abundant, with far less biomass occupied, in the 5-45 kg range than predicted by metabolic scaling. Instead of a mass-abundance relationship that is log-linear with a slope around -0.75, communities exhibit unimodal distributions, with peak abundances in the 45-405 kg mass range (Fig. 2, figs. S6-S8). This reflects the lack of small arboreal primates and forest antelopes in savanna habitats, from which most of our extant and probably all of our fossil communities were sampled. In contrast, extant forest communities show peak abundance at 5-45 kg and effectively log-linear relationships (figs. S7, S9B). When considering only individuals > 45 kg and communities that have at least three size categories occupied (n=54 fossil and 37 extant communities), mass-abundance relationships abide by predictions of metabolic scaling, with slopes close to -0.75 (medians and 95% quantiles: -0.70, -1.48 to -0.03 for fossil; -0.80, -1.76 to 0.20 for extant), and biomass-abundance slopes around 0.25 (0.23, -0.62 to 0.88 for fossil; 0.22, -0.69 to 1.20 for extant, Fig. 2D-E).

Third, between the Late Miocene and the Late Pleistocene there was a reallocation of biomass towards smaller size categories (Fig. 3). Fossil communities experienced a protracted loss of individuals > 400 kg starting in the Pliocene, reflected by increasingly negative mass-abundance and mass-biomass slopes. AIC values favored a breakpoint at 3.8 Ma for both abundance and biomass (95% confidence intervals 5.5–2.1 Ma and 5.3–2.2 Ma, respectively) over a linear model of decrease (difference of greater than 2 AIC units) while a Davies test (which tests for a non-constant regression parameter) was of borderline significance (p=0.07 and 0.04 for abundance and biomass, respectively). The breakpoint model however was neither favored nor significant over a linear model in sensitivity analyses (figs. S11-S15), so the mode of biomass restructuring over time should probably be revisited with a larger dataset. For the time being, our results correspond with the statistically significant 4.6 Ma (5.9–3.3 Ma) breakpoint previously identified for megaherbivore diversity decrease (*6*), as well as with Pliocene breakpoints in multiple environmental proxy records (Fig. 4, discussed below).

Further examining the temporal trend by mass category revealed major losses of individuals > 400 kg since the latest Miocene or Early Pliocene (Fig. 3D). These losses were accompanied by abundance increases or stasis in the 5-405 kg mass range (Fig. 3E). A principal component analysis confirms that the increase in the relative abundance of the 45-135 kg mass categories, and decrease in all other categories, was a major driver of differences over time (figs. S7-S8). Our findings confirm the long-term pattern of megafaunal loss and community restructuring previously described by Faith et al. (*6*, *21*) and indicate continuous and fundamental changes to the distribution of biomass in African large mammal communities over the last 4 myr or more. This result is robust with regard to different sensitivity analyses (*19*). In terms of our hypothetical scenarios, our results falsify both the Truncation and Guillotine models, which predict stable mass-abundance slopes, and support the Twirling Stick model, which predicts progressive changes in slopes over time (Fig. 1).

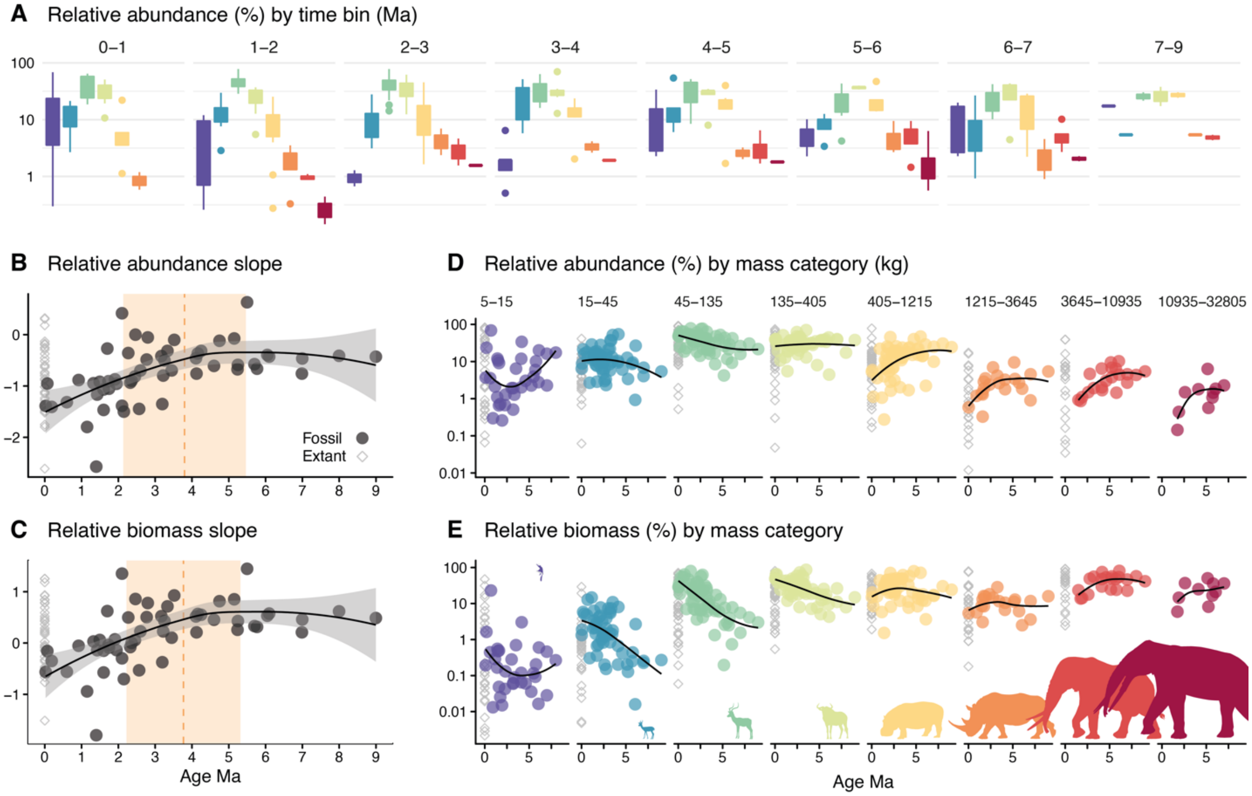


Fig. 3. Changes in mass-abundance and mass-biomass distributions over time. Data points are communities. **A**, Mass-abundance distributions for fossil communities grouped by time bin. **B-C**, Mass-abundance and mass-biomass slopes in fossil communities (>45 kg) decrease over time, reflecting major changes in community size structure starting ~4 Ma. Orange vertical lines and shaded areas indicate breakpoint medians and their 95% confidence intervals. **D-E**, Relative abundance and biomass occupied by each size class over time (same data as A). Note the decreases in the largest sizes and increases in smaller sizes over time, which explains the steepening slopes of panels B-C. Lines of fit (loess) are calculated using fossil data only.

Extinction accelerated by primary productivity loss

The loss of large-sized individuals in the African fossil record coincided with a decrease in global temperature, and, in eastern Africa, with the loss of wooded habitats, and the expansion of C_4 grasslands in (*22–24*), all of which also show statistically significant breakpoints between ~2 and 5 Ma (Fig. 4C-E). Previous studies have also argued for decreasing atmospheric CO_2 and increasing African aridity at this time, though different proxies have provided conflicting signals in these regards (e.g. *25*, *26* and references therein). Just how paleoenvironmental changes may have led to the observed changes in taxonomic and functional community structure is still a topic of debate and speculation. Today, interactions between mammalian herbivores and their physical environments are largely mediated through the plants they consume, such that large mammal herbivore biomass is strongly correlated positively with net primary productivity (NPP) (*27*). Major decreases in NPP since the Late Miocene have previously been recorded in both North America and Europe (*28*, *29*), suggesting a global pattern. Such NPP losses could have significantly diminished the total biomass (carrying capacity) of large mammal communities, thereby reducing diversity and causing megafaunal extinctions following the Guillotine model. In order to determine whether African NPP also decreased since the Late Miocene, we used an established correlation between mammalian community dental morphology and NPP in the present day (*30*, *31*) to estimate NPP in fossil African communities. We found that NPP in the African Late Miocene and Early Pliocene was on average around three times higher than levels measured today (Fig. 4B). A progressive drop in average NPP began in the Early Pliocene (breakpoint at 4.1 ± 0.78 Ma) and continued to recent times, paralleling the losses in megafaunal abundance and biomass noted above. Though they cannot explain the observed changes in mass-abundance distributions (i.e. slopes), such losses in NPP might have reduced mammalian species richness and accelerated the extinction of the largest size categories (Guillotine model) during the Pliocene and Pleistocene (we found no significant relationship between NPP (*32*) and mass-abundance or mass-biomass slopes in extant communities [fig. S16]). Our finding of decreasing mass-abundance slopes in conjunction with losses in NPP therefore suggests a variant of the Twirling Stick model which incorporates both biomass reallocation (the exact cause of which remains unknown) with losses in total carrying capacity (i.e. decreasing slope and intercept) over the last ~4 myr.

Several aspects of our conclusions could be further tested. The declines in NPP for example are based on the mammalian record, and an independent proxy for paleo-NPP would be welcome to confirm the declining trend. Also needed are improvements of climatic proxy records for global paleo-CO_2, and also regional and local vegetation structure, temperature, seasonality, and aridity indices since Late Miocene times. Finally, further work should attempt to more clearly determine the relationships between NPP and biomass distributions in extant communities, despite wholesale alteration of terrestrial ecosystems by humans (*27*). Through such approaches, the proposed link between climatic changes, decreasing productivity, and the global loss of megafauna during the Plio-Pleistocene may be strengthened, potentially also explaining the large declines in Pleistocene population sizes observed in genomes of surviving large mammal species (*11*). Our study supports a growing body of evidence that the effects of Pleistocene human overkill (well-documented in several contexts, especially islands, and especially since 15 ka) (*33*) would have come on top of long-term declines in megafaunal abundance caused by environmental changes. Further work should determine whether the patterns revealed by the African record hold up on other continents as well. Mass-abundance distributions could also provide new insights into size-biased extinctions at other times in Earth's history.

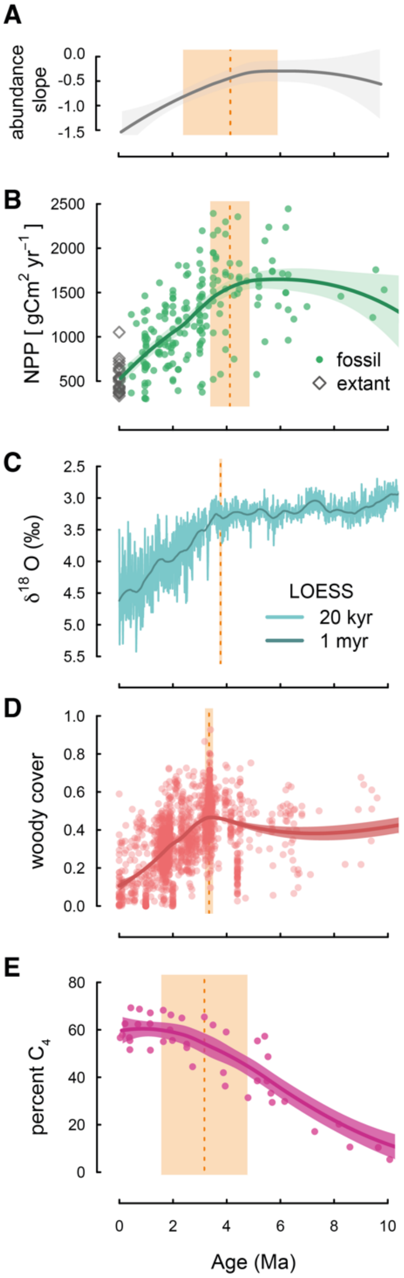


Fig. 4. Environmental context of African megafaunal losses. A, Large mammal community mass-abundance slopes over time (same as Fig. 3C). **B,** Changes in net primary productivity over time, estimated using dental morphology of mammalian molars from 192 African paleocommunities (*31*) and 23 extant African communities (*12*), assessed at the species level. Data suggest a roughly threefold decrease in net primary productivity since ~ 4 Ma. **C**, Global marine stable oxygen isotope curves show decreasing global temperatures after ~ 4 Ma. **D**, Stable carbon isotope ratios from eastern African paleosol carbonates (*22*) converted to fraction woody cover (*22*, *34*) show decreasing proportions of tree cover after 4 Ma. **E**, Terrestrial plant wax biomarkers in marine sediments from the Red Sea and Indian Ocean indicate increasing proportions of C_4 grasses since ~10 Ma (*23*). Orange vertical lines and shaded areas indicate breakpoint medians and their 95% confidence intervals. All breakpoints are statistically significant (i.e. preferred over a linear model) and suggest major environmental changes during the Pliocene, coinciding with community biomass restructuring.

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Supplementary Materials

Materials and Methods

Fig S1 to S16

References (35-271)

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Supplementary Materials for

The Plio-Pleistocene Decline of African Megaherbivores: Long-term losses linked to community biomass restructuring

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This PDF file includes:

Materials and Methods
Tables S1 to S4
Fig S1 to S16
References (35-271)

Other supplementary material for this manuscript includes the following:

Data S1-S2 (csv format)
Data S3-S5 (R format)

The Mammal Dental Metrics Database, available at: doi:10.5061/dryad.69p8cz968

Materials and Methods

Datasets

Dental metrics of African and Arabian fossil and extant large herbivorous mammals (Artiodactyla, Perissodactyla, Proboscidea, and Primates) were compiled from the literature (*35–179*) and by measuring specimens at the Museum für Naturkunde in Berlin. Information on the ages of fossil sites was also compiled from the literature (*47*, *60*, *65*, *69–71*, *89*, *97*, *104*, *124*, *147*, *152*, *155*, *157*, *160*, *161*, *171*, *173*, *180–233*). This dataset, introduced here as the Mammal Dental Metrics Database (*17*), is accessible at doi:10.5061/dryad.69p8cz968. The version used here was downloaded on 6 April 2023. The total dataset has measurements for 52006 teeth from 12148 fossil and 4324 extant specimens. After subsetting to just the orders, tooth positions, and communities used for analyses, these are 13070 teeth from 8941 extant and 4129 fossil specimens. Composition and density of extant large mammal communities were taken from Hatton et al. (*12*). Additionally, census data for African game parks and regions was compiled from the literature and reports found online (*234–265*). Body mass of extant mammal species was taken from the Pantheria database (*18*). Taxonomy for extant species followed the IUCN Red List (https://www.iucnredlist.org). All analyses were conducted in R (v. 4.2.2) (*266*). R code and additional data needed to replicate all analyses are provided as supplementary materials.

Body mass estimation

Body mass for fossil specimens was estimated using a fit of average species body mass to tooth length of modern specimens. Tooth length was chosen because the use of a single metric (in contrast to tooth area, which requires both length and width) means more fossil teeth can be included in any sample (some fragmentary teeth can only be measured in a single dimension). Additionally, previous studies (*140*, *267*, *268*) on the correlation of dental variables with body size in ungulates consistently found that tooth row length was a better predictor of body size than tooth width or area, since “length comes close to being a true size variable, whereas width includes a major component of shape and therefore dietary adaptation” (*268* p. 220). We conducted separate fits for each cheek tooth position, considering only adult cheek teeth (upper and lower second to fourth premolars and first to third molars). An exception was made for extant proboscideans, as these do not possess adult premolars (while many fossil proboscideans do). To permit the estimation of body mass for fossil proboscidean premolars, deciduous premolars of extant proboscideans were included in the adult premolar regressions. Power (loglinear) and quadratic (curvilinear) regressions of average species mass on tooth length were calculated for each tooth position. While biological allometry normally follows a power relationship, we found that a quadratic regression fit the data significantly better for most tooth positions (fig. S2), based on a difference of more than two Akaike Information Criterion (AIC) units (table S1). The reason for this could be that the inclusion of distantly related taxa reveals a higher-order pattern which requires a non-loglinear allometric model (e.g. *269* for a discussion of non-loglinear allometry in biological systems). The best fit for each tooth position was then used to estimate the body mass of fossil specimens. Fossil teeth with ambiguously identified positions (e.g. ‘P2 or P3’; ‘M1 or M2’) were randomly resolved to either position. Teeth identified as just molars (‘M’) were randomly resolved to either M1 or M2, as the third molar is usually straightforward to identify, even when fragmentary. Results did not vary if these ambiguously identified teeth were excluded entirely from the analyses. Body mass estimates from multiple teeth belonging to the same specimen were averaged. Comparison of the estimated specimen mass against predicted specimen mass for extant specimens shows that these largely fall along the 1:1 line, indicating the regressions are performing well (fig. S3). Figure S4 shows estimated mass ranges for fossil specimens by genus, and these are largely within the ranges expected based on size comparisons with closely-related extant representatives. Giraffids are an example of a clade that is notably underestimated.

Figure S5 shows the relationship between tooth length and estimated mass for fossil specimens using different estimation regressions. Using a single fit for all taxa together as described above results in similar slopes across tooth positions and orders (fig. S5A). We also investigated order-specific fits of specimen mass to tooth length. Since these were more taxon-specific, and were based on a smaller number of specimens per fit, we used a power regression only and did not consider quadratic fits. Order-level fits permit varying allometric relationships among clades, and this can be seen in shallower slopes (lower estimates than the single fit) for Primates and Perissodactyla, and steeper slopes (higher estimates) in Artiodactyla (fig. S5B). For Proboscidea, however, the fact that the three extant species are similar in mass, and that teeth of *Elephas maximus* are mostly longer than those of *Loxodonta africana* and *L. cyclotis*, even though the latter species are larger, resulted an overall negative slope (meaning larger teeth are assigned smaller estimated mass, an improbable situation, fig. S5B). Accordingly, we also developed a third option that uses order-level fits for Artiodactyla, Perissodactyla, and Primates, and uses the estimates from the single-fits for Proboscidea (fig. S5C). Sensitivity analyses using the order-level fits, and the order-level+single fit Proboscidea options are described below (main results and conclusions are unaffected by the choice of mass estimate approach).

Community metrics

All specimens were assigned to one of eight logarithmic mass bins spanning 5 to 32,805 kg (the largest estimated specimen mass was 21,161 kg). Fossil communities were defined based on combinations of locality and chronology, often by geological member. Only paleo-communities with more than 20 specimens were considered. Only extant communities with more than six species were retained. To ensure a realistic representation of community mass spectra, only communities with at least three mass bins occupied were included. Calculations of mass-abundance and mass-biomass slopes used only data for mass bins >45 kg, and only communities that had at least three mass bins >45 kg occupied (n=54 communities). Extant communities with data from multiple census years were averaged. Fossil and extant communities are listed in tables S2-S4.

Segmented model (breakpoint) analyses on the fits of abundance and biomass slopes over time (Fig. 3B & C) were conducted using the R package *segmented* (*270*). A Davies test (*238*), which tests for a non-constant regression parameter and is also implemented in the *segmented* package, was used to determine whether the null hypothesis of a linear fit (i.e. no breakpoints) could be rejected in favor of a segmented model.

Sensitivity analyses

In order to gauge the robustness of our results to variations in the quality of the data or analytical parameters, we re-analyzed our data using: 1, Body mass estimates calculated using tooth length and width (i.e. tooth area) instead of tooth length. 2, Monographic sites only instead of all paleo-communities. Monographic sites represent fossil assemblages that have received monographic treatment, meaning the assemblage was generally collected and published by a single team within a relatively short time-frame, which guarantees more even sampling and taxonomic coverage than sites for which publications on different taxa have appeared sporadically over time. 3, Body mass estimates calculated using order-level regressions instead of a single regression for all mammals. 4, Body mass estimates calculated using single-fit regressions for Proboscidea and order-level regressions for Artiodactyla, Perissodactyla, and Primates. 5, Molars only instead of all cheek teeth. The use of molars only avoids biases relating to differing numbers of premolars across different clades (all mammals have three molars in each jaw, but premolar numbers vary between three and none), as well as any impact of using deciduous premolars to estimate body mass for adult premolars in Proboscidea (as described above). The results (figs. S10-15) show that the main conclusions of our analysis are unaffected by these different considerations. The single main result that differed between the main and sensitivity analyses was the age and significance of the abundance and biomass slope age breakpoints.

Net Primary Productivity (NPP)

NPP data for extant communities came from the Socioeconomic Data and Applications Center Human Appropriation of Net Primary Productivity (HANPP) dataset (*32*), available at http://sedac.ciesin.columbia.edu/data/set/hanpp-net-primary-productivity.

The basis of our paleo-NPP estimates is the New and Old Worlds database (*31*). We used information for 111 African localities with at least 5 genera of the orders Perissodactyla, Artiodactyla, Proboscidea, Primates, Tubulidentata and Hyracoidea. The retained fossil communities (n= 192) include 151 genera with 427 species (with between 10 and 44 species per locality), and span between 10.55 Ma and 70 ka. NPP was estimated from living species using information for 23 extant African communities included in Hatton et al. (*12*). For each locality, we computed average hypsodonty (*HYP*) and average longitudinal loph count (*LOPH*) based on species-specific data also obtained from the New and Old Worlds database. These were then used to calculate NPP following the equation given by Liu et al. (*30*):

$$NPP = 2957.8 - 304.3 * HYP - 1043.7 * LOPH$$

To visualize long-term NPP trends, we fit a LOESS curve to the data with an optimal smoothing parameter estimated using AIC values (*271*) (Fig. 4).

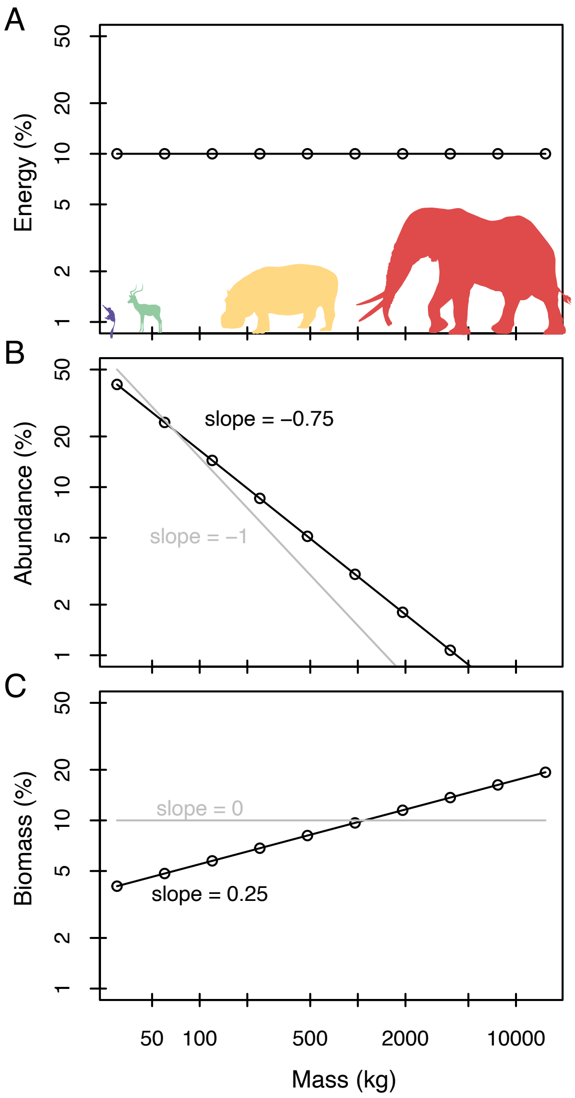


Figure S1. Mass-abundance and mass-biomass distributions under metabolic scaling. A, each mass category within a community uses an equal amount of energy (E, y-axis units are arbitrary). **B,** abundance per unit area (i.e. density, N) is determined as $N = M^{-0.75}$, and the mass-abundance distribution is log-linear with a slope of -0.75. **C,** the biomass (B) of each mass category is N x M, which equates to $B = M^{0.25}$, giving a mass-biomass slope of 0.25. Larger-sized species may be less abundant on the landscape, but they produce a relatively more individuals and biomass per unit energy consumed than smaller species do. Grey lines show a scenario under which there is no metabolic advantage to being large ($N=M^{-1}$, $B=M^{0}$).

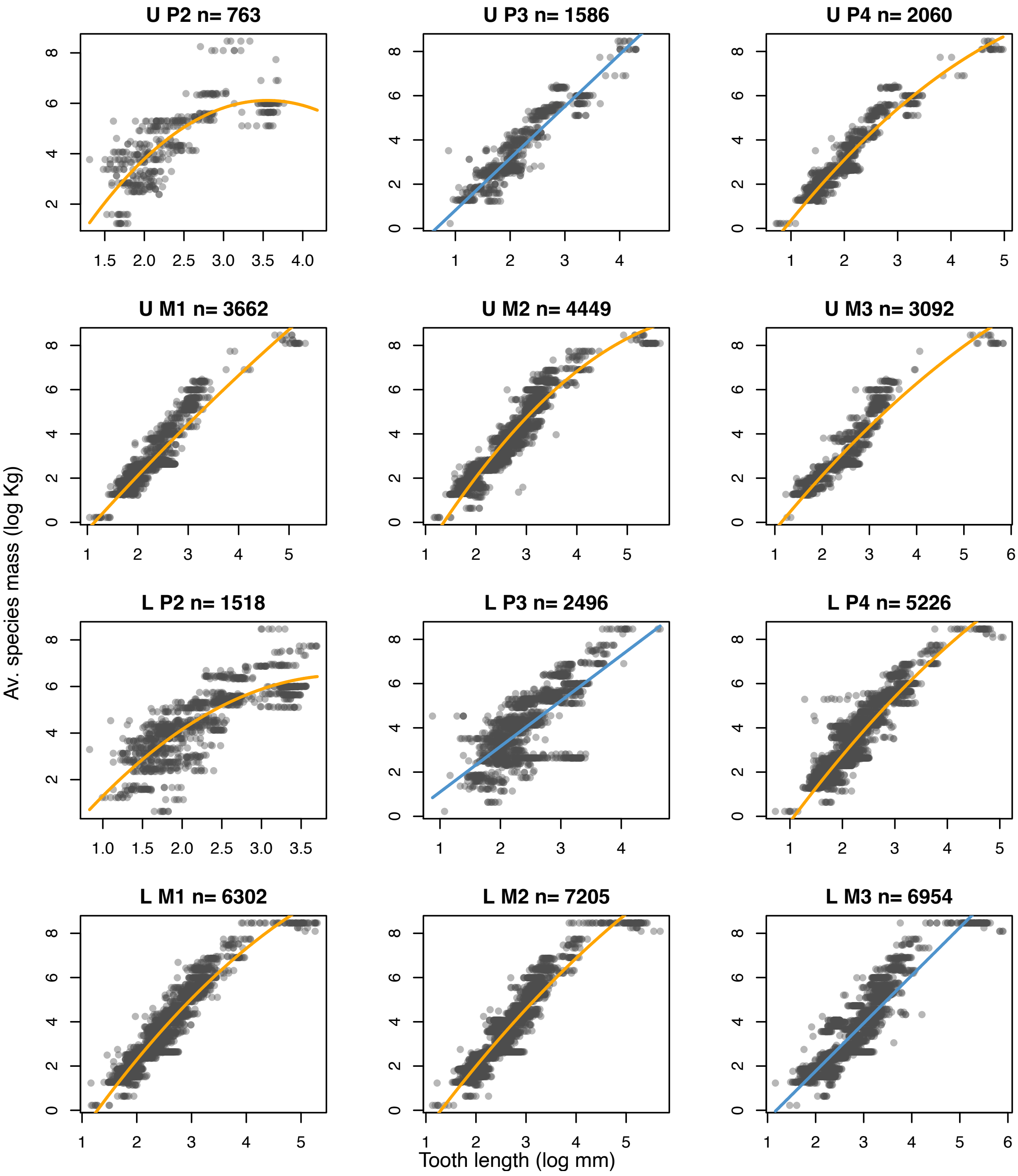


Figure S2. Fits of average species mass against log tooth length in extant specimens. Each plot represents a single tooth position (L, lower; M, molar; P, premolar; U, upper; n, sample size). Note that premolar data include deciduous premolars for Proboscidea, as the extant representatives of this order do not possess adult premolars. Quadratic regressions (orange) fit the data better than power regressions (blue) for most tooth positions (Table S1). These fits were used to estimate body mass for fossil teeth.

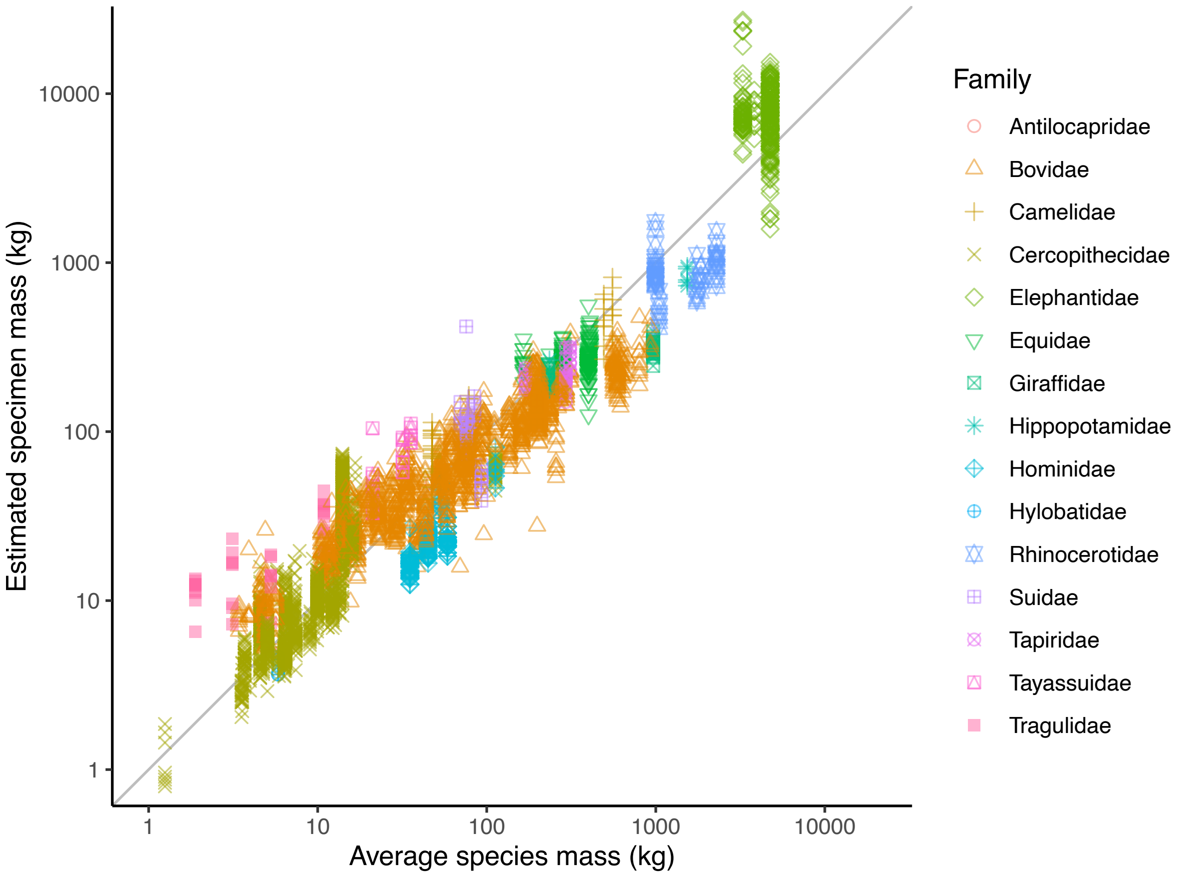


Figure S3. Estimated body mass vs. average species mass for extant specimens. These are the same specimens used in the previous figure, with estimates based on different teeth from the same specimen averaged. The data are scattered around the 1:1 line (grey), indicating that the predictions work well across taxa. Rhinocerotids, giraffids, and large bovids are generally underestimated, while tragulids and small bovids are generally overestimated.

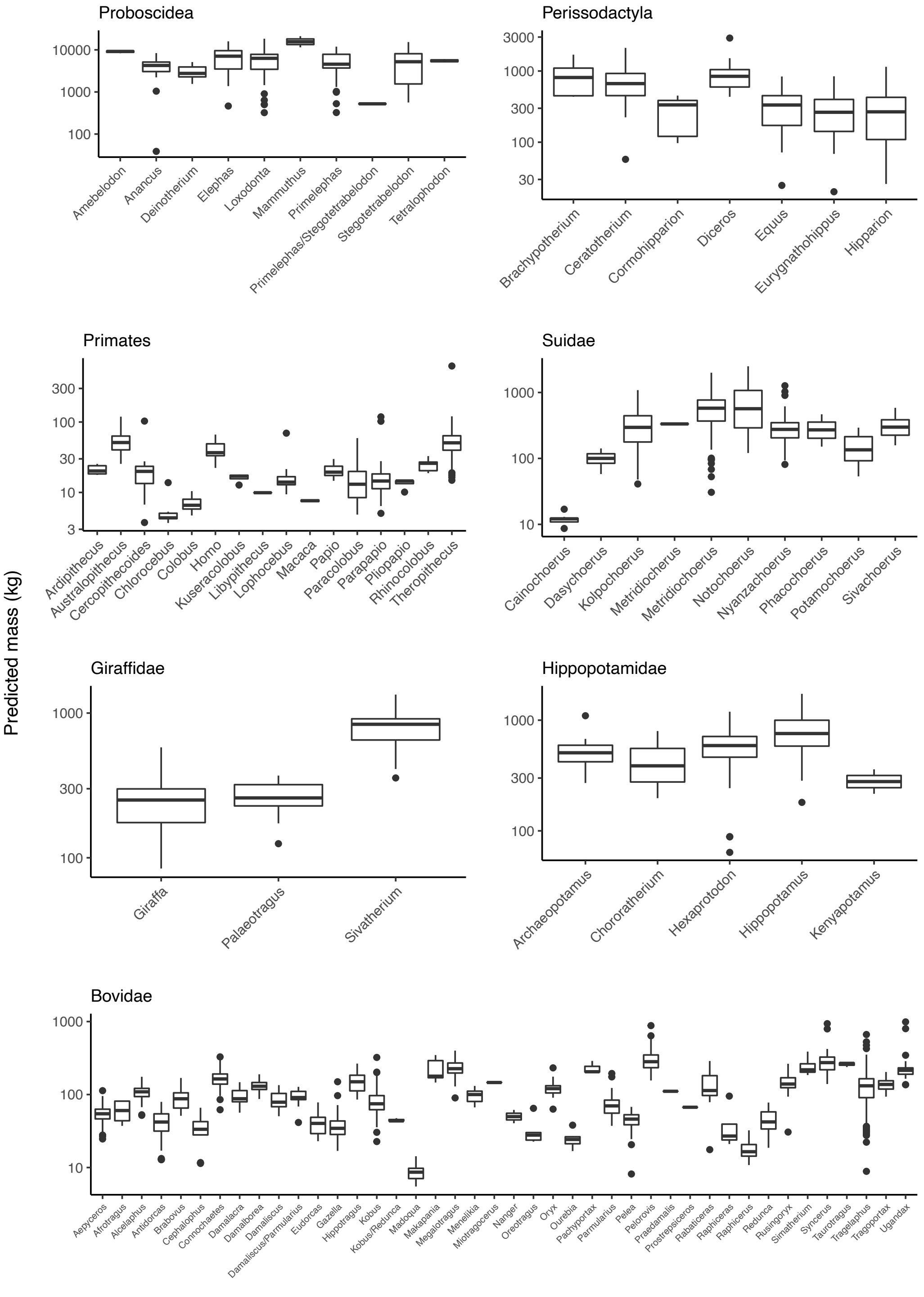


Figure S4. Body mass estimates for fossil specimens by genus. Despite some variation, most estimates are within the range expected based on size comparisons with closely-related extant representatives. Giraffids are notably underestimated.

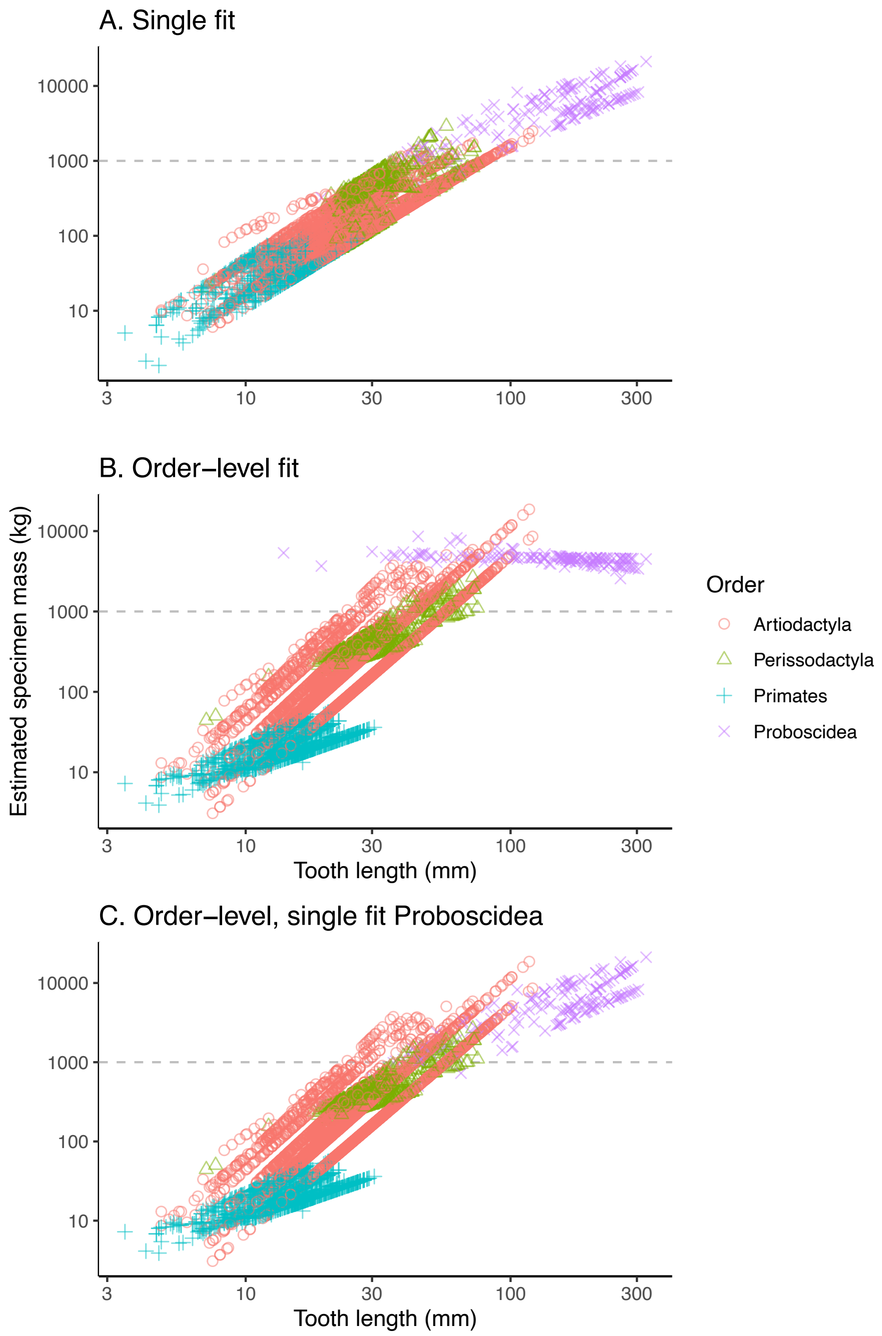


Figure S5. Estimating body mass from tooth length in fossil specimens using different estimation approaches. A, using fits for all taxa together (as in Fig. S2) results in a similar relationship for all orders. **B**, using order-level fits produces shallower slopes (lower estimates) in Primates and Perissodactyla, steeper slopes in Artiodactyla, and unchanging or even negative slopes in Proboscidea. **C**, using estimates from order-level fits for Artiodactyla, Primates, and Perissodactyla and from single fits for Proboscidea is perhaps the best option, but since it results in higher abundances of very large individuals (>1000 kg), we conservatively chose to use the single-fit regressions for our main analyses. Using options B or C provides similar results (figs. S13 and S14)

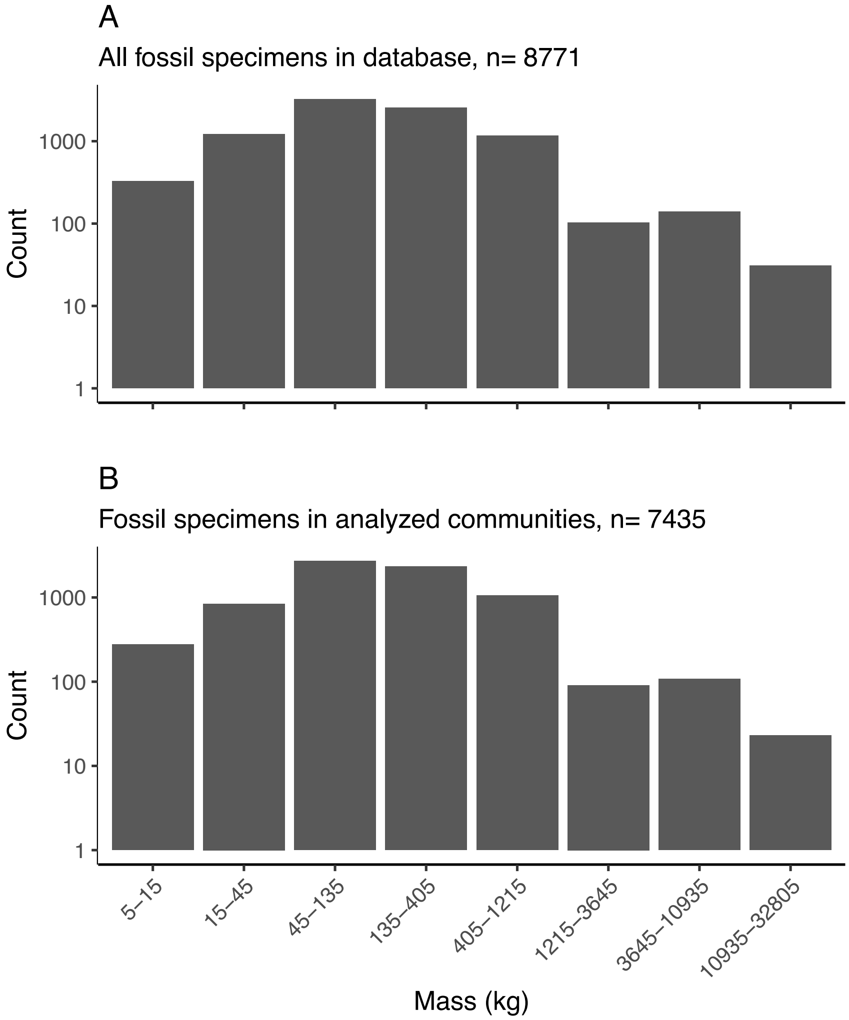


Figure S6. Mass-abundance distribution of fossil specimens. A, Absolute counts of all fossil specimens of Artiodactyla, Perissodactyla, Proboscidea, and Primates in the Mammal Dental Metrics Database for which mass could be estimated. **B,** Only those specimens belonging to communities that were analyzed. Whether analyzing the entire dataset or subsetting by community, mass-abundance relationships in African fossil large mammals show unimodal distributions, with a peak in the 45-135 kg mass range.

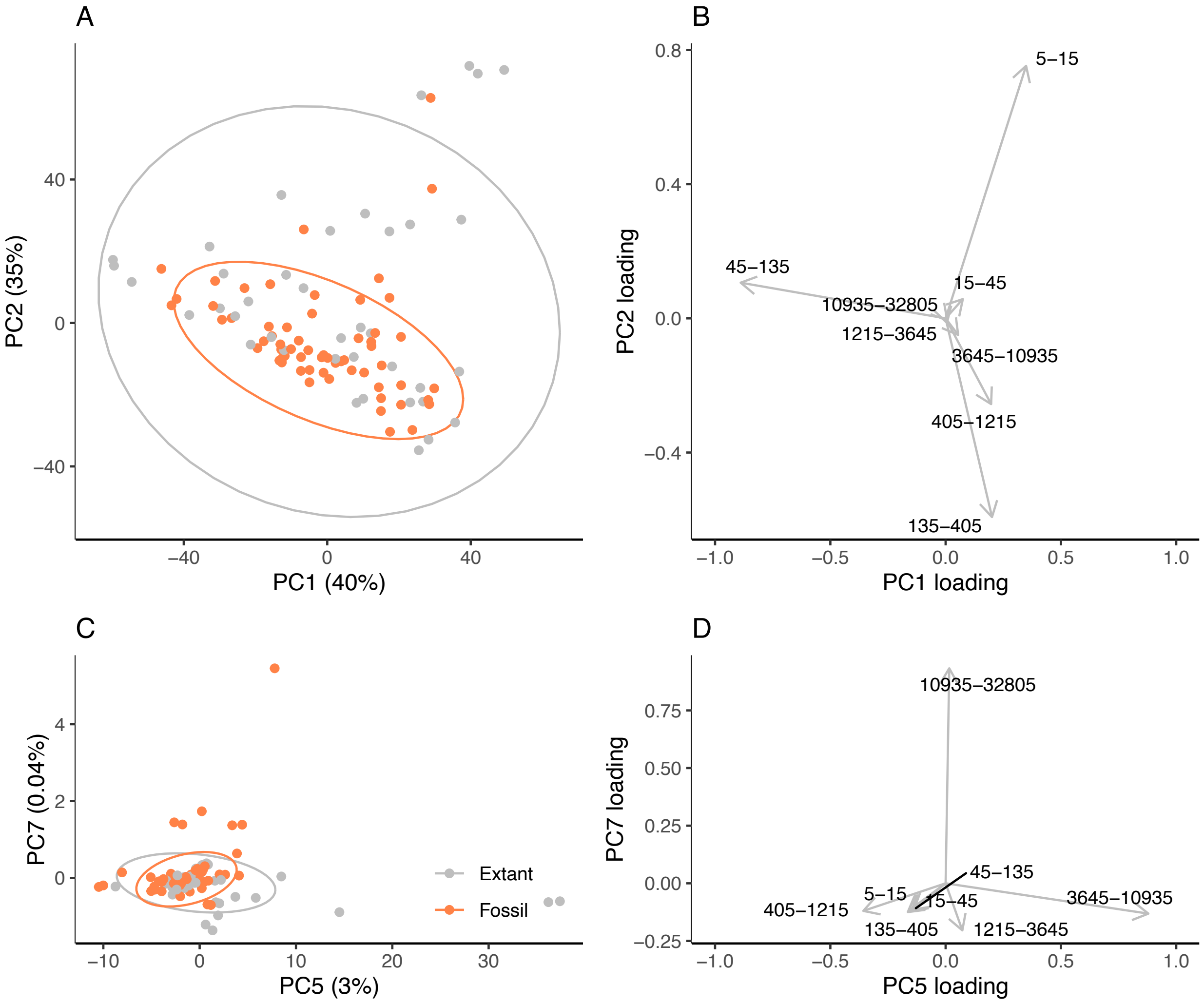


Figure S7. Principal component analysis of relative abundance of mass categories in extant and fossil communities. A, Fossil communities fall within the 95% ellipse of extant communities along the first two components (which explain 74% of the variance), indicating similar relative abundance distributions. **B,** Eigenvectors show that four extant communities (Afrotropical forest, Buxa Tiger Reserve, India, Neotropical forest, and Palamau Tiger Reserve) are distinguished by significantly higher proportions of the smallest size category (5-15 kg), which mainly comprises arboreal monkeys and forest antelopes. The remaining extant and fossil communities are from savanna faunas, which are low in mammals < 15 kg. **C-D**, Individuals > 3645 kg have the greatest loadings on PC5 and 7. Four extant communities show the highest proportions of individuals in the ~3600 - 10,000 kg category (due to elephants; Okavango Delta, Hwange, Gonarezhou, Mkomazi), while six fossil communities are particularly abundant in individuals > 10,000 kg (Baynunah, Kanapoi, Sahabi, Langebaanweg, Ndolanya Beds Upper, Nawata Upper). Fig. S9 shows mass-abundance distributions for all communities.

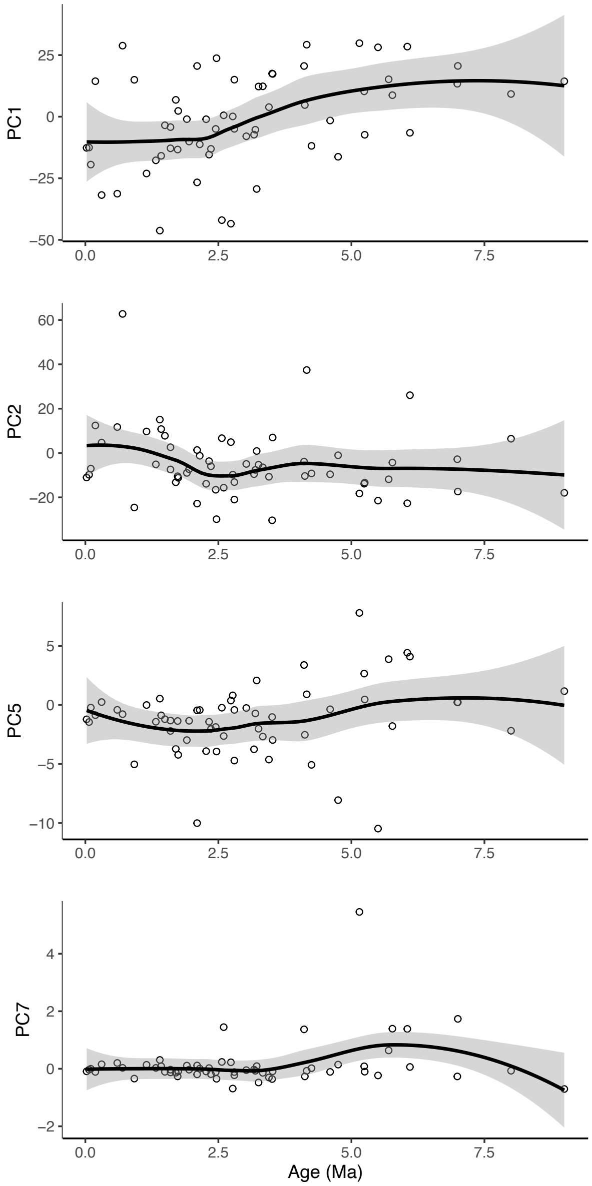
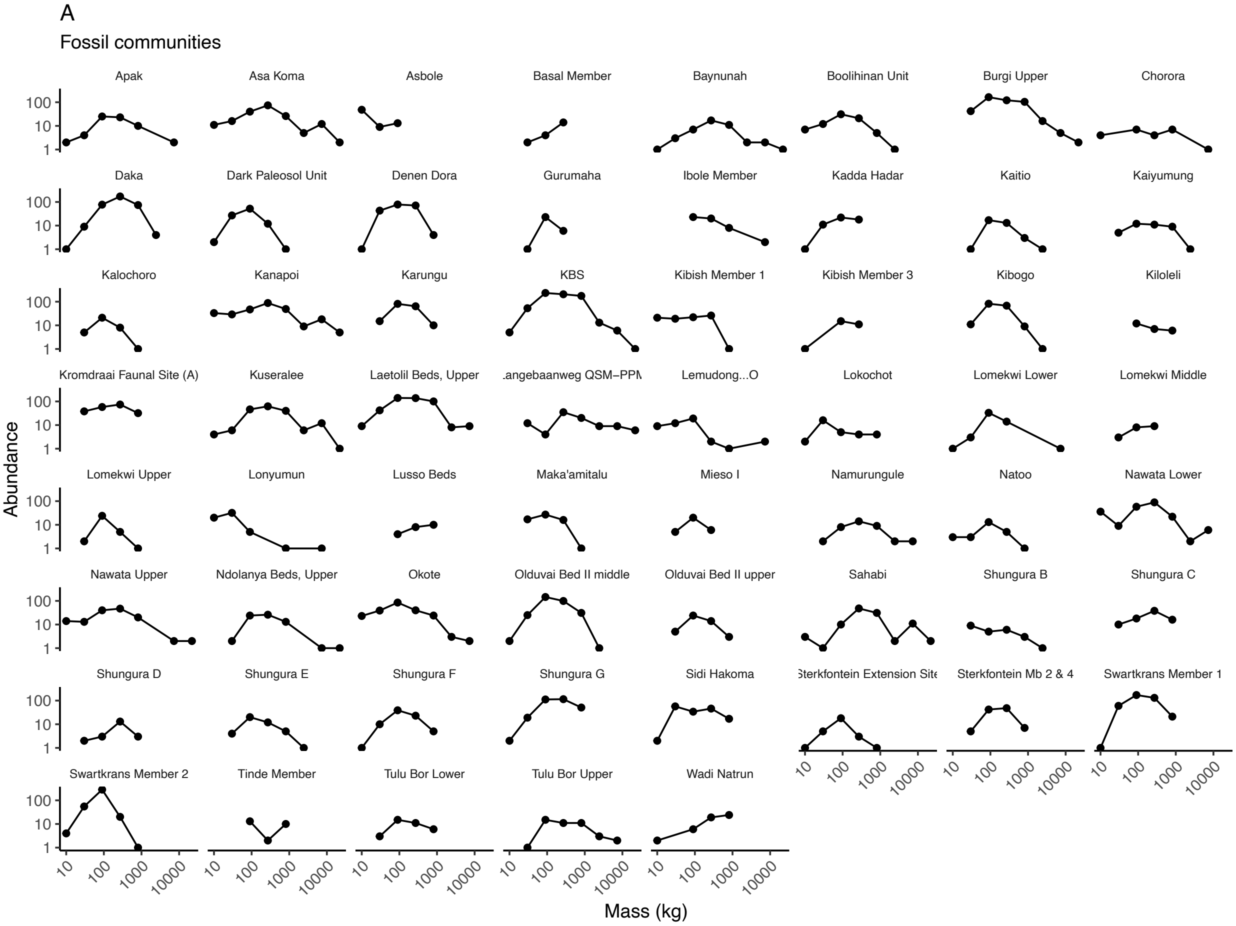
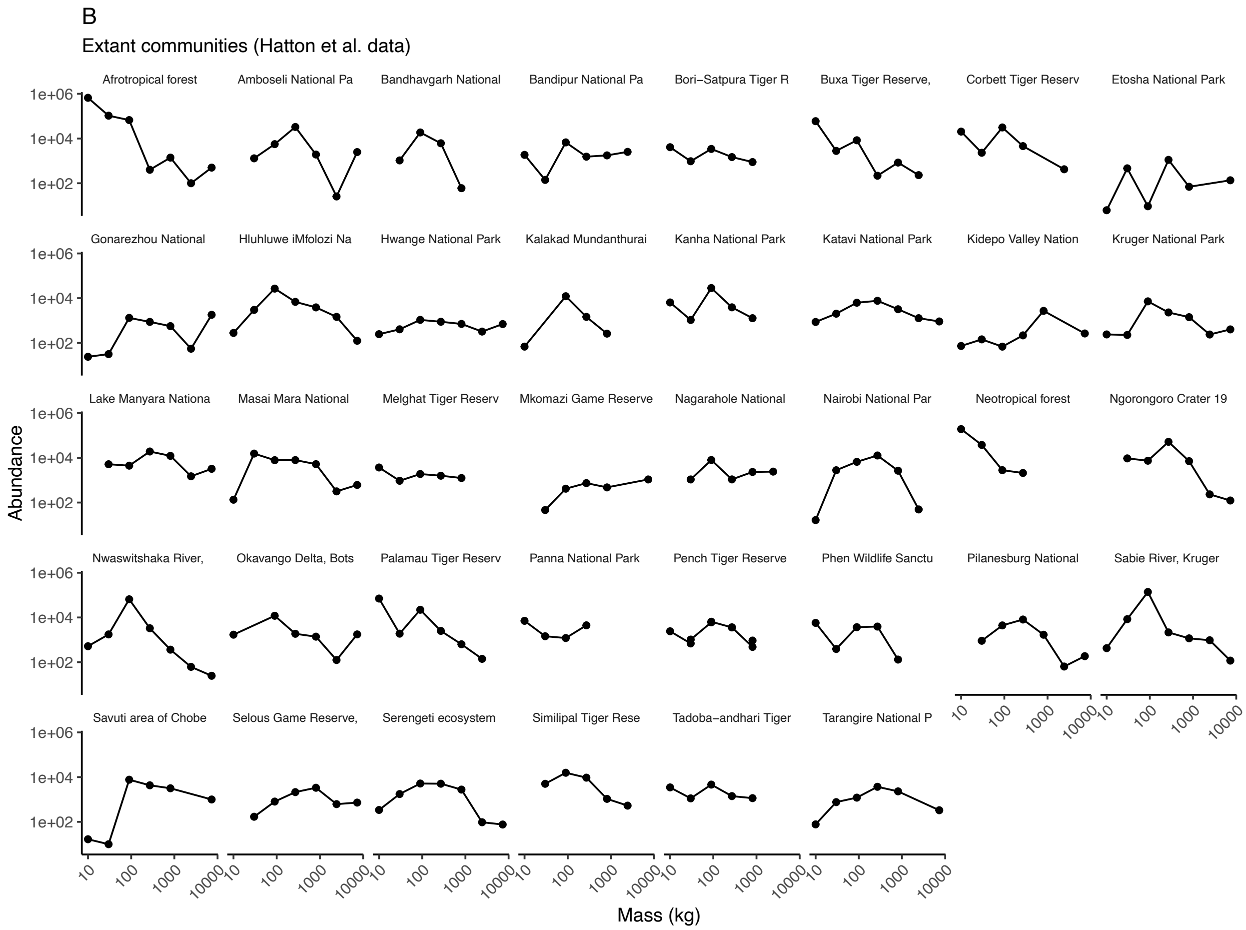


Fig. S8. Changes over time in the principal components shown in the previous figure. The major change, mirroring that of the abundance and biomass slope values in Fig. 3, occurs along the first principal component (PC1), which reflects increases over time in the relative abundance of individuals with mass 45-135 kg, and relative decreases in all other mass categories.


A
Fossil communities
Apak
Asa Koma
Asbole
Basal Member
Baynunah
Boolihinan Unit
Burgi Upper
Chorora
Daka
Dark Paleosol Unit
Denen Dora
Gurumaha
Ibole Member
Kadda Hadar
Kaitio
Kaiyumung
Kalochoro
Kanapoi
Karungu
KBS
Kibish Member 1
Kibish Member 3
Kibogo
Kiloleli
Kromdraai Faunal Site (A)
Kuseralee
Laetolil Beds, Upper
.angebaanweg QSM−PPM
Lemudong...O
Lokochot
Lomekwi Lower
Lomekwi Middle
Lomekwi Upper
Lonyumun
Lusso Beds
Maka'amitalu
Mieso I
Namurungule
Natoo
Nawata Lower
Nawata Upper
Ndolanya Beds, Upper
Okote
Olduvai Bed II middle
Olduvai Bed II upper
Sahabi
Shungura B
Shungura C
Shungura D
Shungura E
Shungura F
Shungura G
Sidi Hakoma
Sterkfontein Extension Site
Sterkfontein Mb 2 & 4
Swartkrans Member 1
Swartkrans Member 2
Tinde Member
Tulu Bor Lower
Tulu Bor Upper
Wadi Natrun
Abundance
100
10
1
10
100
1000
10000
Mass (kg)


B
Extant communities (Hatton et al. data)
Afrotropical forest
Amboseli National Pa
Bandhavgarh National
Bandipur National Pa
Bori–Satpura Tiger R
Buxa Tiger Reserve,
Corbett Tiger Reserv
Etosha National Park
Gonarezhou National
Hluhluwe iMfolozi Na
Hwange National Park
Kalakad Mundanthurai
Kanha National Park
Katavi National Park
Kidepo Valley Nation
Kruger National Park
Lake Manyara Nationa
Masai Mara National
Melghat Tiger Reserv
Mkomazi Game Reserve
Nagarahole National
Nairobi National Par
Neotropical forest
Ngorongoro Crater 19
Nwaswitshaka River,
Okavango Delta, Bots
Palamau Tiger Reserv
Panna National Park
Pench Tiger Reserve
Phen Wildlife Sanctu
Pilanesburg National
Sabie River, Kruger
Savuti area of Chobe
Selous Game Reserve,
Serengeti ecosystem
Similipal Tiger Rese
Tadoba–andhari Tiger
Tarangire National P
1e+06
1e+04
1e+02
Abundance
10
100
1000
10000
Mass (kg)

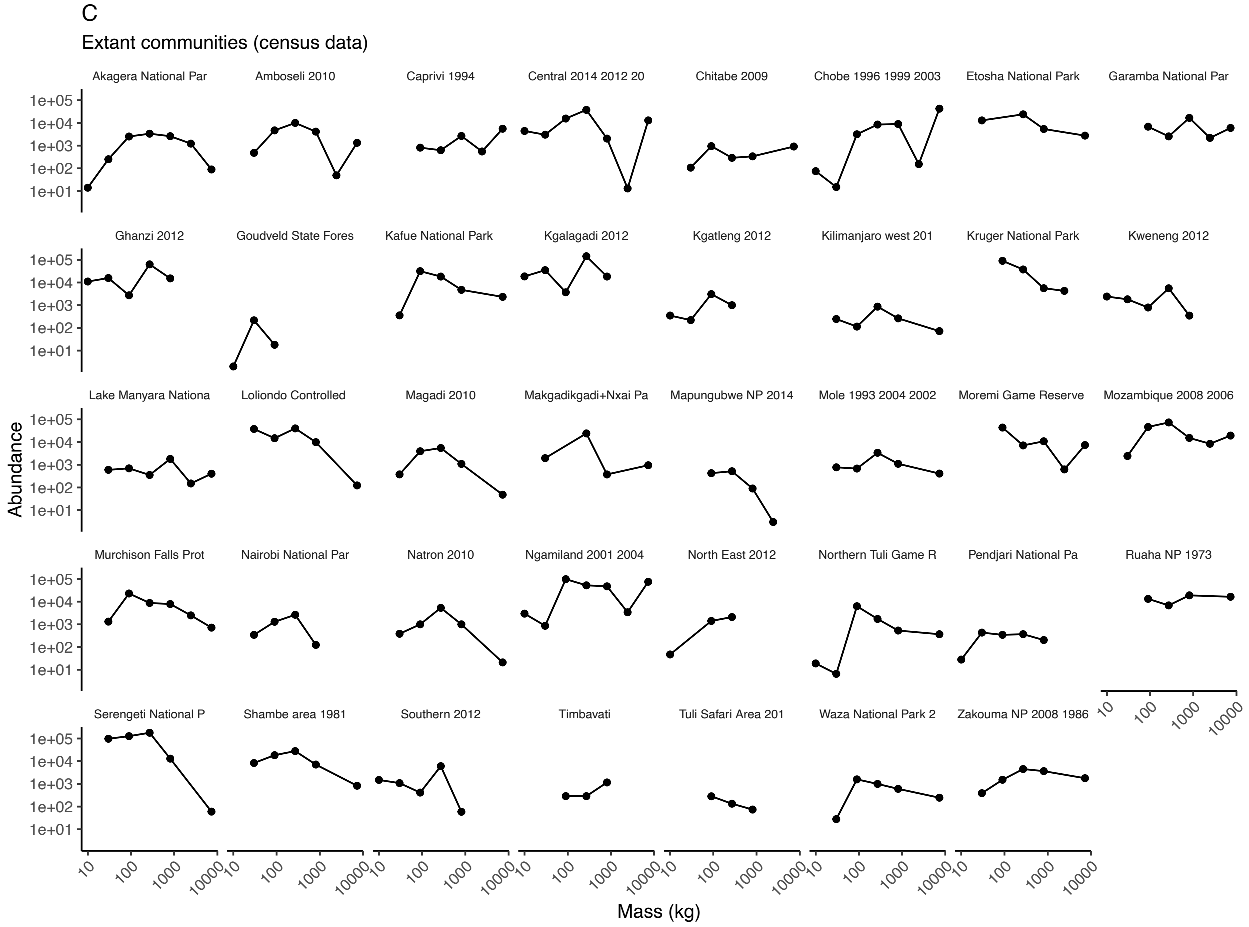


Figure S9. Community mass-abundance distributions. A, fossil communities. **B,** extant large mammal communities from the Hatton et al. dataset (*12*). **C,** extant African large mammal communities from a compilation of census data (this study). Abundance here is the absolute number of individuals. Note that almost all communities show unimodal distributions, with peaks in the 45-405 kg range. Four forest communities in **B** (Afrotropical forest, Buxa Tiger Reserve, Neotropical forest, and Palamau Tiger Reserve) are notable exceptions and show essentially log-linear distributions.

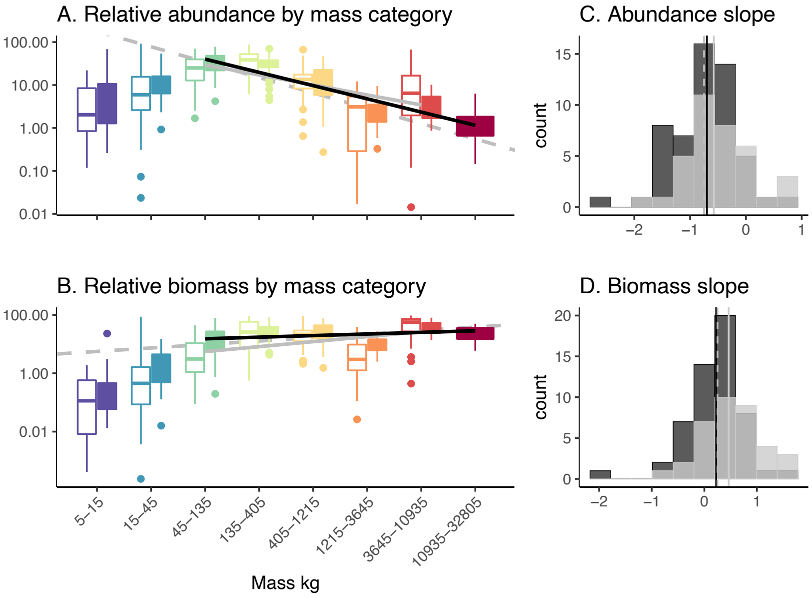


Figure S10. Mass-abundance and mass-biomass distributions in fossil and extant large mammal communities. Same as Fig. 2 in main text, except using a compilation of African census data (this study) for extant communities instead of the Hatton et al. (*12*) dataset. Results are similar regardless of the extant dataset used. Note the lower variation of the 5-15 kg category (A-B, compare with Fig. 2A-B), reflecting the lack of forest habitats in the census data. As in Fig. 2, filled boxplots and the darker histograms and lines represent fossil data.

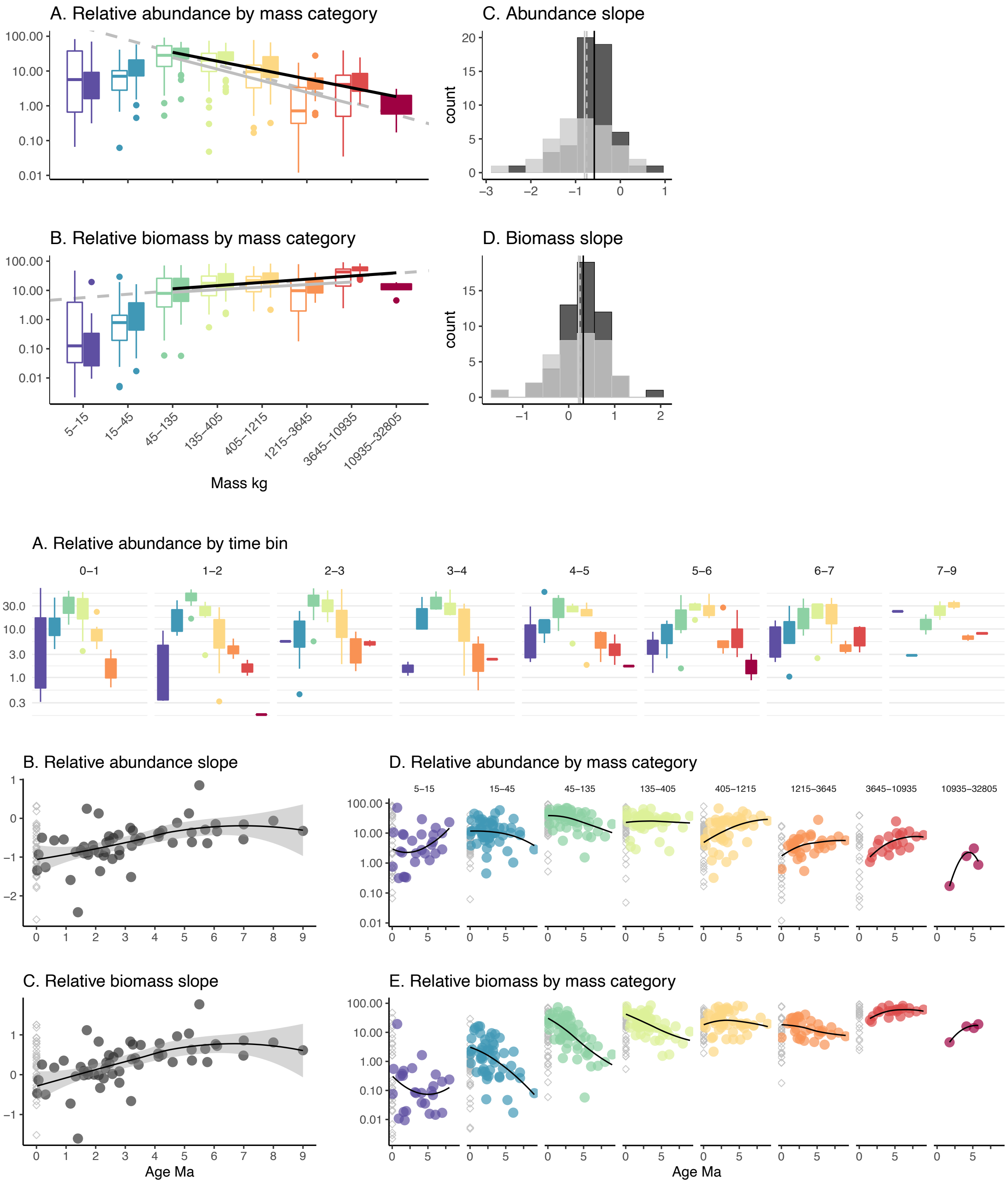


Figure S11. Results of sensitivity analysis 1. Same as Figs. 2-3, except using tooth area (length x width) instead of tooth length to estimate body mass. The main difference from Figs. 2-3 is that the abundance and biomass slope curves no longer show statistically significant breakpoints (a linear model of decrease is preferred). As in Fig. 2, filled boxplots and the darker histograms and lines represent fossil data.

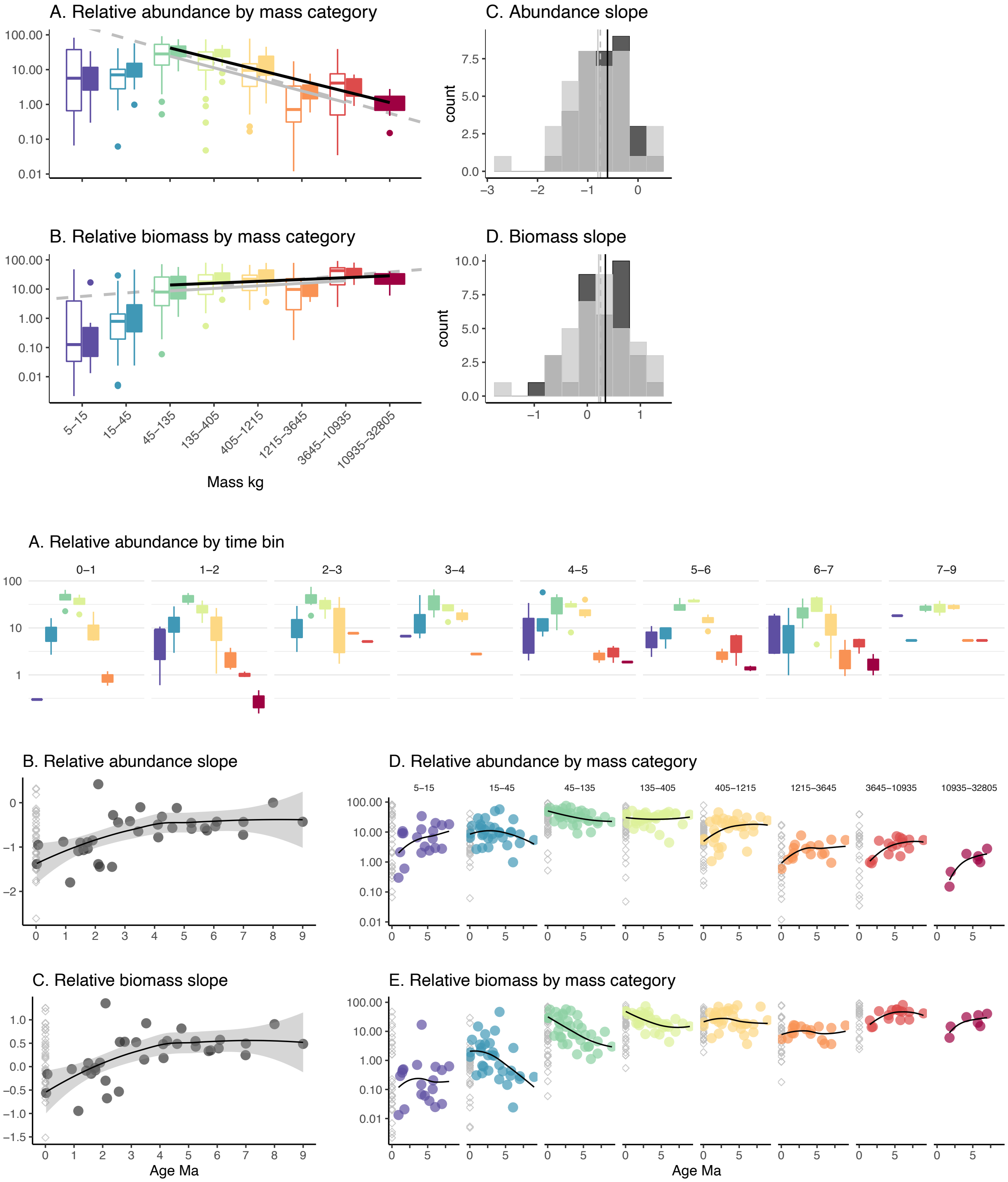


Figure S12. Results of sensitivity analysis 2. Same as Figs. 2-3, except using only communities which were published following monographic treatment, which should represent more even taxonomic sampling. The main difference from Figs. 2-3 is that the abundance and biomass slope curves no longer show statistically significant breakpoints (a linear model is preferred). As in Fig. 2, filled boxplots and the darker histograms and lines represent fossil data.

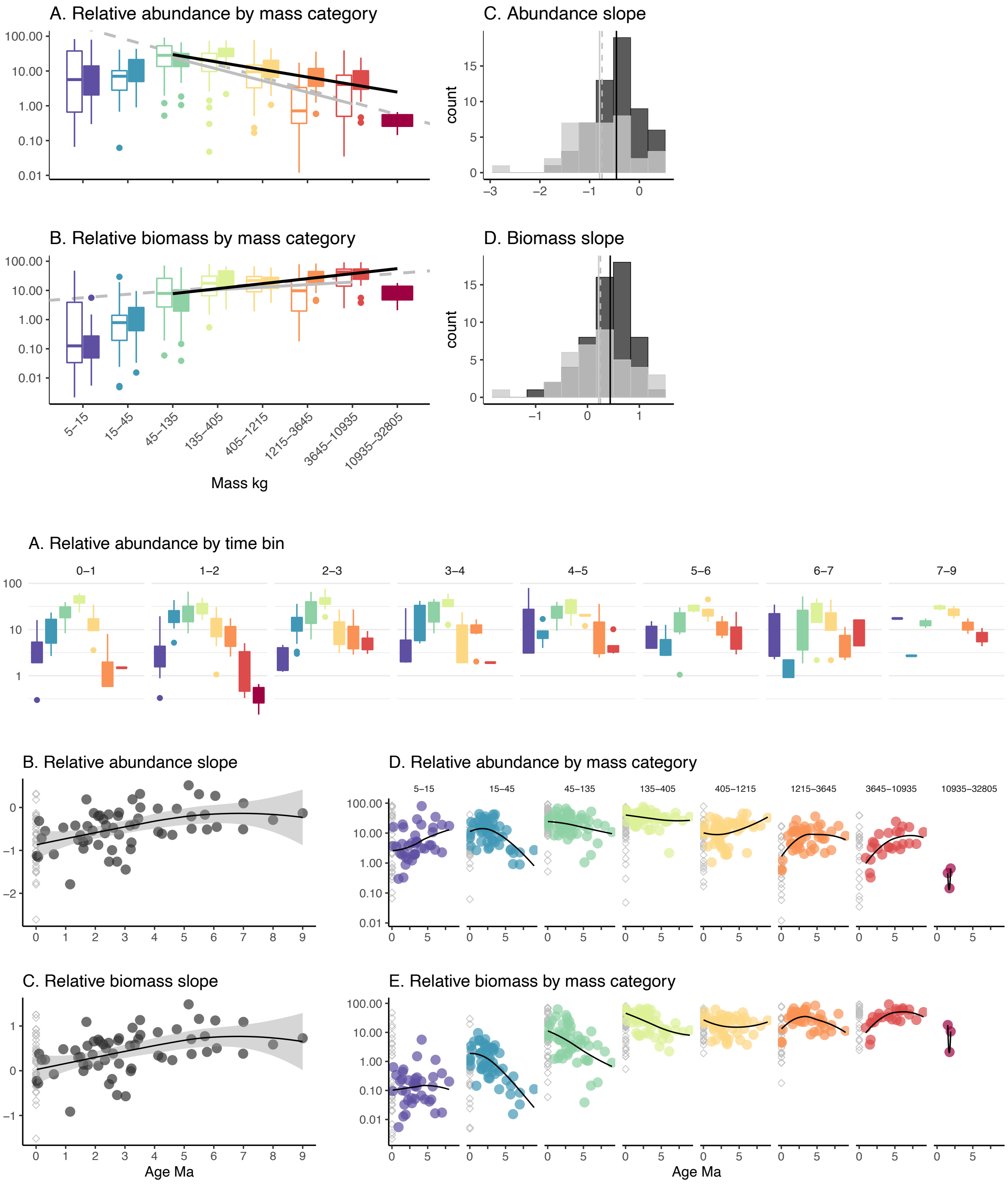


Figure S13. Results of sensitivity analysis 3. Same as Figs. 2-3, except using order-level regressions to estimate fossil specimen body mass. These regressions produce a very limited range of mass estimates for Proboscidea (Fig. S5B), in effect reducing the influence of this clade on the results. The main differences from Figs. 2-3 are the lower proportion of individuals > ~10,000 kg, and that the abundance and biomass slope curves no longer show statistically significant breakpoints (a linear model is preferred). As in Fig. 2, filled boxplots and the darker histograms and lines represent fossil data.

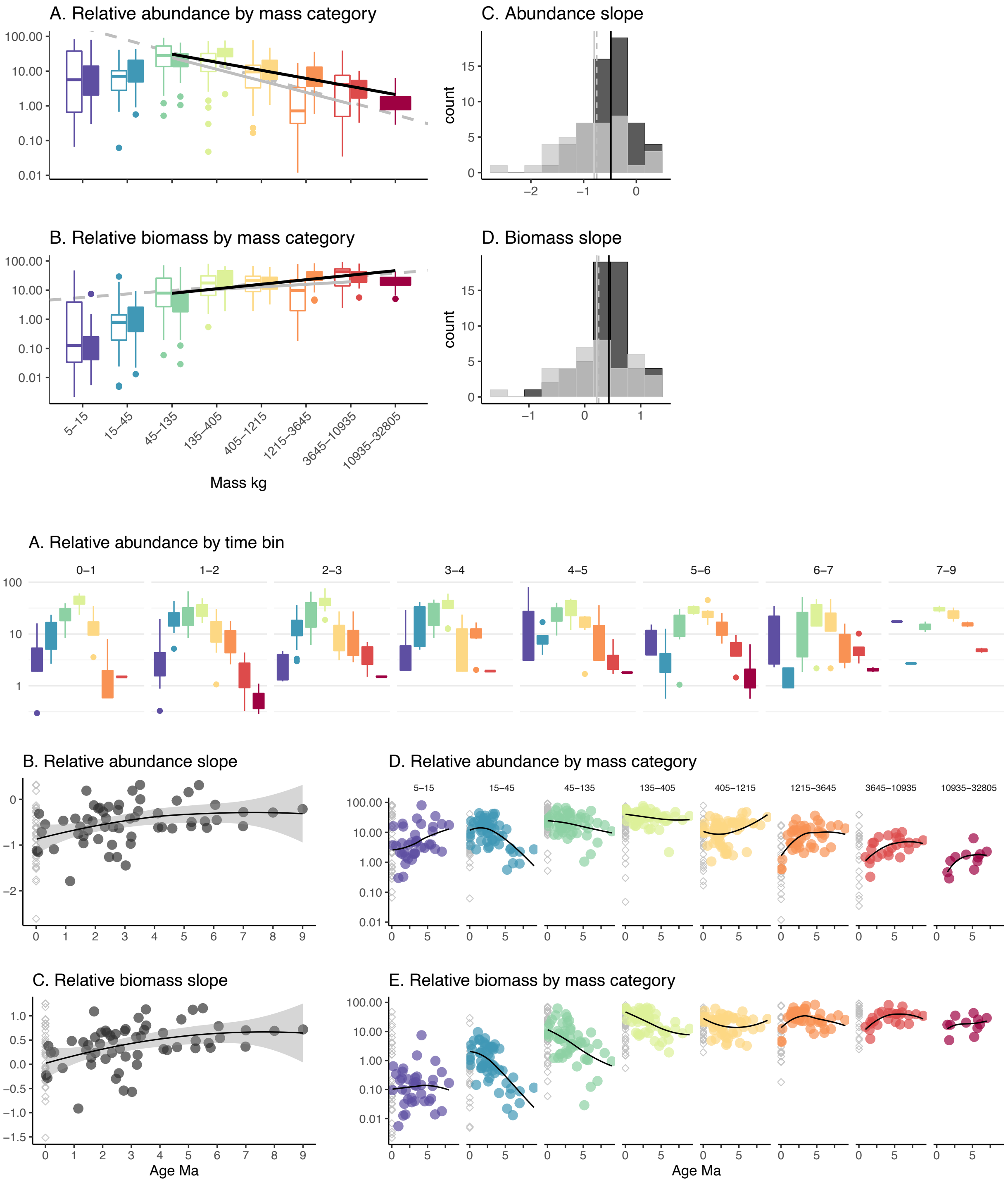


Figure S14. Results of sensitivity analysis 4. Same as Figs. 2-3, except using single-fit regressions to estimate fossil specimen body mass for Proboscidea and order-level regressions for Artiodactyla, Perissodactyla, and Primates (Fig. S5C). The main difference from Figs. 2-3 is that the abundance and biomass slope curves no longer show statistically significant breakpoints (a linear model is preferred). As in Fig. 2, filled boxplots and the darker histograms and lines represent fossil data.

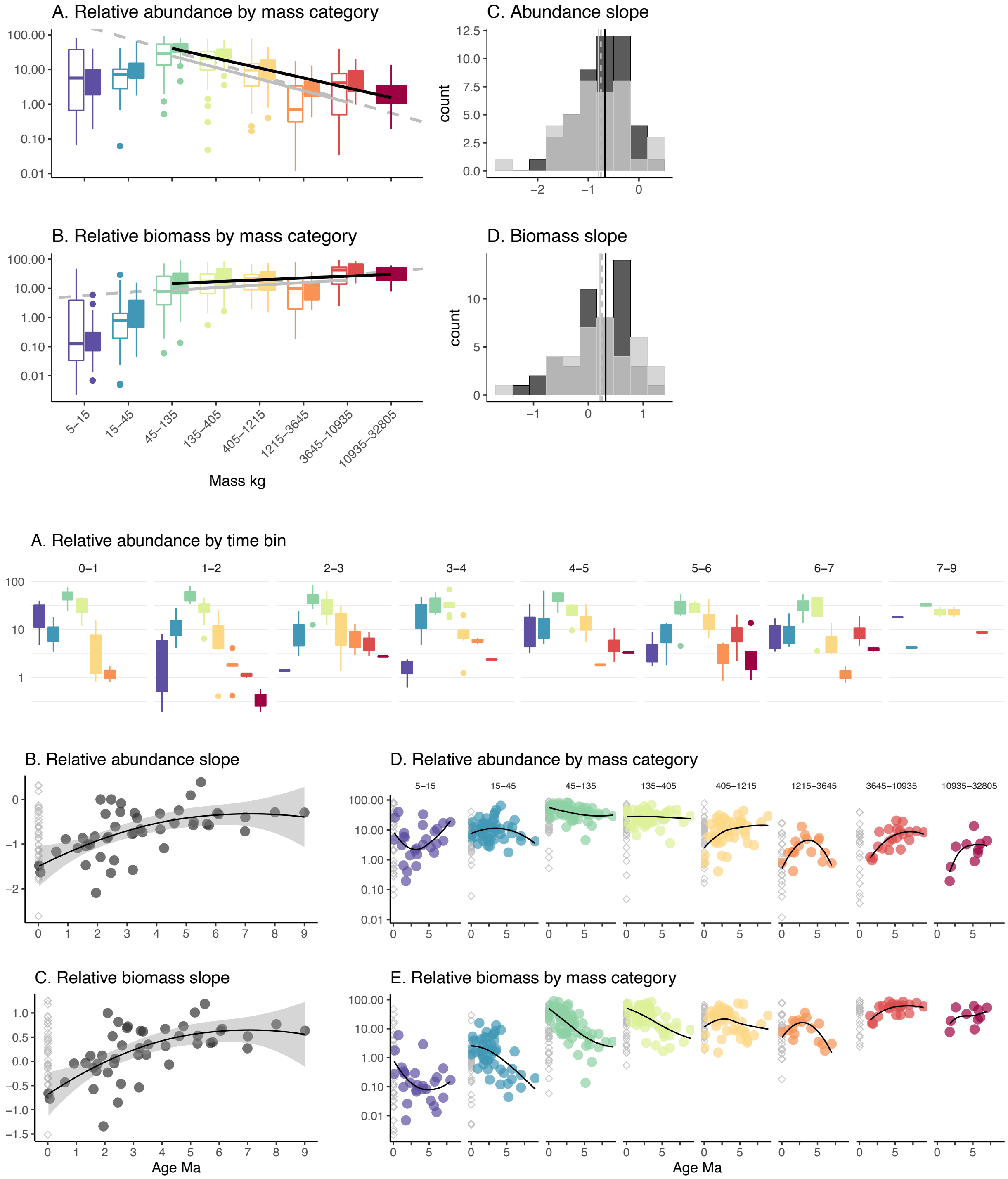


Figure S15. Results of sensitivity analysis 5. Same as Figs. 2-3, except using fossil molars only (no premolars). The main difference from Figs. 2-3 is that the abundance and biomass slope curves no longer show statistically significant breakpoints (a linear model is preferred). As in Fig. 2, filled boxplots and the darker histograms and lines represent fossil data.

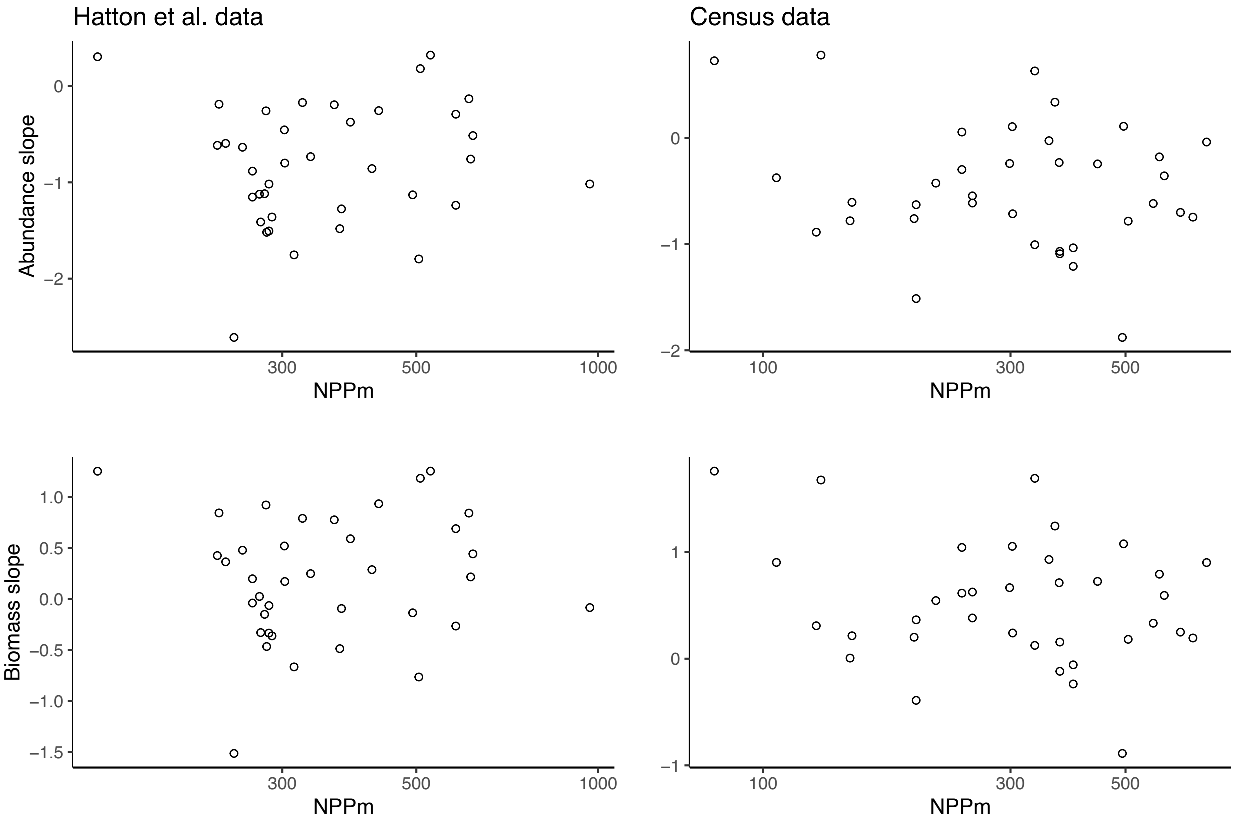


Fig. S16. Relationship between mass-abundance and mass-biomass slope values and net primary productivity in extant communities. Whether using the Hatton et al. (*12*) or census compilation dataset (this study), all correlations are not significant ($p>0.05$). NPPm, mean NPP (in millions of grams of carbon) calculated for a 1x1° grid surrounding the coordinates of each community (*32*). As in Fig. 3, slope values are calculated only for mass categories >45 kg.

Table S1. Difference of Akaike Information Criterion (AIC) values between quadratic and power fits of average extant species body mass against specimen tooth length (Fig. S2). The quadratic fit is significantly better for all tooth positions except for the upper and lower third premolars and the lower third molar (AIC difference > -2).

Upper/Lower	**Tooth position**	**AIC quadratic**	**AIC power**	**Δ AIC**
U	P2	1153	1215	-62
U	P3	1534	1532	2
U	P4	1720	1854	-135
U	M1	3620	3631	-10
U	M2	4122	4675	-553
U	M3	2181	2233	-52
L	P2	3002	3081	-79
L	P3	5014	5013	1
L	P4	6944	7032	-88
L	M1	6275	6621	-346
L	M2	8103	8239	-136
L	M3	8125	8125	0

Table S2. Name, location, and maximum and minimum ages (in Ma) of fossil communities. e indicates age is estimated. A more detailed version of this table including references is provided as supplementary data.

	Community	**Country**	**Age max**		**Age min**	
1	Apak	Kenya	5	e	4.2	
2	Asa Koma	Ethiopia	5.8		5.6	
3	Asbole	Ethiopia	0.8	e	0.6	e
4	Basal Member	Ethiopia	3.6	e	3.42	
5	Baynunah	United Arab Emirates	8		6	
6	Boolihinan Unit	Ethiopia	1.7	e	1.5	e
7	Burgi Upper	Kenya	1.945	e	1.87	
8	Chorora	Ethiopia	9		7	
9	Daka	Ethiopia	1.04		0.8	
10	Dark Paleosol Unit	Ethiopia	1.4	e	0.9	e
11	Denen Dora	Ethiopia	3.24	e	3.15	e
12	Gurumaha	Ethiopia	2.82		2.65	
13	Ibole Member	Tanzania	5.5	e	5	e
14	Kadda Hadar	Ethiopia	3.15	e	2.9	
15	Kaitio	Kenya	1.87		1.6	
16	Kaiyumung	Kenya	3.9	e	3	
17	Kalochoro	Kenya	2.33		1.87	
18	Kanapoi	Kenya	4.11		4.11	
19	Karungu	Kenya	0.094	c	0.045	c
20	KBS	Kenya	1.88		1.61	
21	Kibish Member 1	Ethiopia	0.196		0.18	e
22	Kibish Member 3	Ethiopia	0.13		0.075	
23	Kibogo	Kenya	0.036		0.012	

24	Kiloleli	Tanzania	4.5	e	4	e
25	Kromdraai Faunal Site (A)	South Africa	1.8		1.6	
26	Kuseralee	Ethiopia	5.3	e	5.18	
27	Laetolil Beds, Upper	Tanzania	4.4		3.85	
28	Langebaanweg QSM-PPM	South Africa	5.25		5.05	
29	Lemudong,ÄôO	Kenya	6.12		6.08	
30	Lokochot	Kenya	3.6		3.44	
31	Lomekwi Lower	Kenya	3.44		3	e
32	Lomekwi Middle	Kenya	3	e	2.6	e
33	Lomekwi Upper	Kenya	2.6	e	2.53	
34	Lonyumun	Kenya	4.35	e	3.97	
35	Lusso Beds	Democratic Republic of Congo	2.3		1.9	
36	Maka'amitalu	Ethiopia	2.4		1.9	
37	Mieso I	Ethiopia	0.4	e	0.212	
38	Namurungule	Kenya	9		9	
39	Natoo	Kenya	1.55	e	1.3	
40	Nawata Lower	Kenya	7.44		6.54	
41	Nawata Upper	Kenya	6.54		5	e
42	Ndolanya Beds, Upper	Tanzania	2.6		2.6	
43	Okote	Kenya	1.61		1.38	
44	Olduvai Bed II middle	Tanzania	1.7	e	1.5	e
45	Olduvai Bed II upper	Tanzania	1.5	e	1.15	
46	Sahabi	Libya	6.8		5.3	
47	Shungura B	Ethiopia	3.44		3.07	
48	Shungura C	Ethiopia	3.07		2.53	
49	Shungura D	Ethiopia	2.53		2.4	e
50	Shungura E	Ethiopia	2.4	e	2.32	

51	Shungura F	Ethiopia	2.34	2.31	
52	Shungura G	Ethiopia	2.31	2.23	
53	Sidi Hakoma	Ethiopia	3.42	3.25	
54	Sterkfontein Extension Site	South Africa	0.7	0.5	e
55	Sterkfontein Mb 2 & 4	South Africa	2.8	2.1	
56	Swartkrans Member 1	South Africa	2.3	1.6	
57	Swartkrans Member 2	South Africa	1.7	1.1	
58	Tinde Member	Tanzania	5	4.5	e
59	Tulu Bor Lower	Kenya	3.44	2.9	e
60	Tulu Bor Upper	Kenya	2.9	2.64	
61	Wadi Natrun	Egypt	6.5	4.5	

Table S3. Extant communities from the Hatton et al. (*12*) dataset. Community name also includes the census years(s), if given. More detailed information and data sources can be found in the original reference.

	Community	**Country**
1	Afrotropical forest	
2	Amboseli National Park, Kenya; 2007	Kenya
3	Bandhavgarh National Park 1989 1990 1991 1992 1993 1994 1995 1997 1998 1996	India
4	Bandipur National Park 1991 1993 1995 1997	India
5	Bori-Satpura Tiger Reserve 1992 1994 1982 1984 1998 1986 2002 1988 1990 1996	India
6	Buxa Tiger Reserve, India; 1995	India
7	Corbett Tiger Reserve 1995 1997 1993	India
8	Etosha National Park, Namibia; 1998	Namibia
9	Gonarezhou National Park, Zimbabwe; 2009	Zimbabwe
10	Hluhluwe iMfolozi National Park 1982 2000	South Africa
11	Hwange National Park 1996 1973	Zimbabwe
12	Kalakad Mundanthurai Tiger Reserve, India; 1997	India
13	Kanha National Park 1997 1998 1996 1995 1994	India
14	Katavi National Park, Tanzania; 2009	India
15	Kidepo Valley National Park, Uganda; 2009	Uganda
16	Kruger National Park 2009 1964 1975 1984 1997	South Africa
17	Lake Manyara National Park 1970 1992	Tanzania
18	Masai Mara National Reserve 1992 2003	Kenya
19	Melghat Tiger Reserve 1997 1995 1993 1996	India
20	Mkomazi Game Reserve, Tanzania; 1970	Tanzania
21	Nagarahole National Park 1989 2002	India
22	Nairobi National Park 2002 1966 1976	Kenya
23	Neotropical forest	
24	Ngorongoro Crater 1997 2004 1965 1978 1988	Tanzania
25	Nwaswitshaka River, Kruger NP, South Africa; 1975	South Africa

26	Okavango Delta, Botswana; 2008	Botswana
27	Palamau Tiger Reserve 1996 1993 1994 1995	India
28	Panna National Park 1995 1993 1996 1998 1997	India
29	Pench Tiger Reserve (MP) 1990 1991 1992 1993 1995 1996 1994 1997	India
30	Pench Tiger Reserve (MR) 1993 1994 1996 1998 1997	India
31	Phen Wildlife Sanctuary 1994 1995 1996 1997 1998	India
32	Pilanesburg National Park, South Africa; 2000	South Africa
33	Sabie River, Kruger NP, South Africa; 1975	South Africa
34	Savuti area of Chobe National Park, Botswana; 1991	Botswana
35	Selous Game Reserve, Tanzania; 1994	Tanzania
36	Serengeti ecosystem 1993 2003 1971 1977 1986	Tanzania
37	Similipal Tiger Reserve, India; 1997	India
38	Tadoba-andhari Tiger Reserve 1994 1997 1995 1996	India
39	Tarangire National Park 1962 2000	Tanzania

Table S4. Extant African communities compiled from census data for this study. Community name also includes the census years(s). Further details including references are provided as supplementary data.

	Community	**Country**
1	Akagera National Park 2013 2015	Rwanda
2	Amboseli 2010	Kenya
3	Caprivi 1994	Namibia
4	Central 2014 2012 2010	Botswana
5	Chitabe 2009	Botswana
6	Chobe 1996 1999 2003 2002 2001 2004 2006 2014 2011 2010 1993 1994 2012	Botswana
7	Etosha National Park 2015 2005	Namibia
8	Garamba National Park 1998 1991 2003 1993 2002 2000 2012 1986 2004 1995 2007 2006 2005	Democratic Republic of Congo
9	Ghanzi 2012	Botswana
10	Goudveld State Forest 1978-1981	South Africa
11	Kafue National Park 2002 2006 2011	Zambia
12	Kgalagadi 2012	Botswana
13	Kgatleng 2012	Botswana
14	Kilimanjaro west 2010	Tanzania
15	Kruger National Park 2004 1999 2002 2003 2000 2001 2005 1998	South Africa
16	Kweneng 2012	Botswana
17	Lake Manyara National Park 1970 1975 1976 1961 1965 1959 1967 1981 1984	Tanzania
18	Loliondo Controlled Area 1968	Tanzania
19	Magadi 2010	Kenya
20	Makgadikgadi+Nxai Pans 2004 2002 1993 2014 2006 1994 2010 1999 2001 1996 2003	Botswana

21	Mapungubwe NP 2014	South Africa
22	Mole 1993 2004 2002	Ghana
23	Moremi Game Reserve 1993 1994	Botswana
24	Mozambique 2008 2006	Mozambique
25	Murchison Falls Protected Area 1980 2010 1995 2005 1999 2002 1991	Uganda
26	Nairobi National Park 1966 1962 1961 1963	Kenya
27	Natron 2010	Tanzania
28	Ngamiland 2001 2004 2006 1999 2010 1996 2014 2012 2002 2003	Botswana
29	North East 2012	Botswana
30	Northern Tuli Game Reserve 1987 1986 2014 1989 2010 1984 1991 1993 2012 1997 2001 1983 1988 2008 2007 1999 1995 1996	Botswana
31	Pendjari National Park 2000	Benin
32	Ruaha NP 1973	Tanzania
33	Serengeti National Park 1971 1958	Tanzania
34	Shambe area 1981	South Sudan
35	Southern 2012	Botswana
36	Timbavati	South Africa
37	Tuli Safari Area 2014	Zimbabwe
38	Waza National Park 2007	Cameroon
39	Zakouma NP 2008 1986 2002 1991 1995	Chad

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