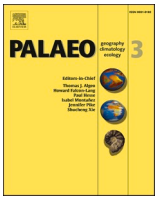
Palaeogeography, Palaeoclimatology, Palaeoecology 643 (2024) 112181

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo



# Ecometric models of small mammal hypsodonty can estimate paleoprecipitation across eastern Africa

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ARTICLE INFO

Editor: Howard Falcon-Lang

*Keywords:*
Ecometrics
Glires
Hypsodonty
Trait-environment relationships
Paleoprecipitation

ABSTRACT

Ecometric analyses use the relationships between functional traits and the environment at the community level to quantitatively estimate past climatic and environmental variables at fossil sites. Hypsodonty (tooth crown height) in North American rodent and lagomorph (Glires) communities is correlated with mean annual temperature and annual precipitation. Here, we examine the community hypsodonty of African Glires to test if this relationship translates to a continent with more extreme climates and to quantify paleoprecipitation at important fossil sites. Categorical hypsodonty values were gathered from the literature and museum collections for 94 modern African taxa (88%). We used maximum likelihood to model the ecometric relationship between hypsodonty and annual precipitation. We then produced trait-based estimates of paleoprecipitation for 26 well-sampled fossil localities from eastern Africa over the last 5.7 Ma. We confirmed other regional studies by identifying increasing aridity and decreasing annual precipitation (824 mm to 480 mm) in the Late Miocene of Kenya. From the Ethiopian Shungura Formation, we estimated temporal fluctuations in precipitation that correspond with the presence or absence of paleolakes and rivers. Small mammal community hypsodonty illustrates that east African communities have converged towards mesodont means and high standard deviations in response to climate change.

## 1. Introduction

Changes in temperature and precipitation will cause certainenvironments to become unrecognizable and uninhabitable by some of the taxa found there today. Anthropogenic climate change has led to warming that is predicted to continue accelerating over the next 100 years (Westerhold et al., 2020). Humans have altered the landscape through expanding resource use, which in turn, has led to habitat loss and increased severity of many natural disasters, like hurricanes, floods, and wildfires (Nagy et al., 2018; Pielke et al., 2005). Biodiversity is greatly threatened by the outcome of these trends, with species being forced to quickly adapt to new climates or attempt to track preferable climates across a fragmented landscape (McGuire et al., 2016). Species unable to efficiently disperse or adapt will face extirpation, or total extinction, and will alter community assembly and functioning across ecosystems. By examining the relationships between fauna and climate through time, we can better anticipate how communities may respond to present and future climatic changes (Barnosky et al., 2017).

While Africa has experienced a range of past climatic events including periods of fluctuating temperatures and precipitation (Couvreur et al., 2021; Diamond and Hamilton, 1980; Tierney et al., 2015), the continent is now facing rapid, diverse, nonuniform changes in temperatures, sea-level rise, and extreme droughts and floods, (Tierney et al., 2015; World Meteorological Organization, 2020). Africa's landscape hosts the largest desert in the world, tropical rainforests, savannas, and glaciated mountains creating incredibly diverse faunal assemblages across the continent (Burgess et al., 2007a, 2007b; Couvreur et al., 2021; Goldblatt, 1978; Jenkins et al., 2013; Linder et al., 2012). Within each of

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https://doi.org/10.1016/j.palaeo.2024.112181
Received 7 December 2023; Received in revised form 1 April 2024; Accepted 1 April 2024
Available online 3 April 2024

these regions, fauna and flora have become uniquely adapted to these extreme climate conditions (Bigalke, 1968; Cloudsley-Thompson, 1989; Heslop-Harrison, 2011). Therefore, future climate trends pose a great risk to these specialized taxa.

Africa contains a rich fossil history of floral and faunal assemblages across a variety of environments through deep time, making it an excellent study system for investigating past faunal responses, both spatially and temporally (Bobe, 2006a; Louchart et al., 2009; Manthi and Winkler, 2020; Reed, 2008; Rowan et al., 2016; Werdelin and Sanders, 2010; Wood and Leakey, 2011). Some sites also preserve well-sampled continuous stratigraphic layers, like the Shungura Formation, which documents changes through time from a single location (Bibi et al., 2013; Boisserie et al., 2008). The fossil record of eastern Africa has been extensively studied in the context of community assembly and hominin evolution, with sites spanning the Late Pleistocene (Bedaso et al., 2010) to the Pliocene (Bobe et al., 2007; Clark Howell et al., 1987; Faith et al., 2015; Gibert et al., 2022; Reed and Geraads, 2012; Su and Harrison, 2015) and containing records of early hominins, large and small mammals, amphibians, and reptiles (Brochu and Storrs, 2012; Head and Müller, 2020; Rage and Bailon, 2011). In addition to faunal records, isotopic analyses (Bedaso et al., 2010; Faith et al., 2015; Su and Harrison, 2015), phytoliths, and pollen records (Adeleye et al., 2022) have been used as proxies for understanding past environments at certain sites. While a variety of proxies have been used to piece together the environment at these sites, there is still a need for generating quantitative paleoclimate estimates that can be easily compared across a range of African localities.

Ecometric analyses make use of the quantitative relationships between functional traits and the environment at the community level. Species are able to live in environments that are suited to their specific functional traits (Messier et al., 2010). When traits are no longer suitable for an environment, species must either adapt, relocate, or risk extirpation and, eventually, extinction (Polly and Head, 2015). Ecometrics is a unique method because it allows for analyses across sites with varying environments and throughout time (Eronen et al., 2010a, 2010b; Faith et al., 2020; Fortelius et al., 2014; Lawing et al., 2017; Lawing et al., 2017; Polly et al., 2011; Polly and Head, 2015; Schap et al., 2021; Short and Lawing, 2021; Vermillion et al., 2018; Žliobaitė et al., 2018). Previous ecometric studies have explored the relationship between temperature and leaf shape and size (Box, 1996; Royer et al., 2005), precipitation and herbivore dental morphology (Eronen et al., 2010b, 2010c; Evans, 2013; Fortelius et al., 2016; Fortelius et al., 2002; Schap et al., 2021; Short et al., 2021; Žliobaitė et al., 2018), vegetation cover and limb proportions in artiodactyls and carnivorans (Barr, 2017; Dunn and Avery, 2021; Polly, 2010; Short et al., 2023; Short and Lawing, 2021), and microvegetation and vertebral proportions and tail length in snakes (Lawing et al., 2012). Estimates of paleoclimate generated from this method can complement estimates from isotopes or pollen and help to parse out environmental variables from sites previously described as mosaic sites, which are sites described as having a wide range of habitats (i.e. a mosaic of Acacia savanna and scrub, savanna woodlands, grasslands, and moist woodlands (Manthi and Winkler, 2020). Ecometric models of these relationships provide useful tools for bridging the gap from the paleontological record to modern communities (Eronen et al., 2010a).

Tooth crown height, or hypsodonty, has been extensively studied because of its correlations with vegetation consumption and climatic changes (Davis and Pineda-Munoz, 2016; Fortelius et al., 2002; Galbrun et al., 2018; Janis, 2008; Janis, 1988; Liu et al., 2012; Pineda-Munoz and Alroy, 2014; Žliobaitė et al., 2018). Originally, an increase in tooth crown height was tied to the spread of fibrous silica-rich grasslands (Damuth and Janis, 2011; MacFadden, 1997; Stirton, 1947; Strömberg, 2002; Webb, 1977), however, it has also been suggested that the relationship is more nuanced and may also be associated with increased exogenous grit and dust settling on vegetation in arid climates (Damuth and Janis, 2014; Damuth and Janis, 2014; Janis, 1988; Jardine et al., 2012; Jernvall and Fortelius, 2002; Semprebon et al., 2019; Williams and Kay, 2001). Taller tooth crown heights with larger surface areas reduce the negative impacts of wear caused by an abrasive diet in species that are consuming large amounts of exogenous grit and other abrasives (Damuth and Janis, 2014; Janis, 1988; Semprebon et al., 2019; Strömberg, 2002). Due to the slow morphological shifts required to alter tooth crown heights and the exceptional preservation of teeth in the fossil record, hypsodonty is a dietary proxy that is useful on an evolutionary time scale (Davis and Pineda-Munoz, 2016) and therefore, can be used to estimate paleoclimate from local fauna preserved in paleontological records.

As an ecometric trait, hypsodonty has been successfully used to explore the relationship between tooth crown height and precipitation in herbivorous mammals (Eronen et al., 2010b, 2010c; Fortelius et al., 2016; Fortelius et al., 2014; Schap et al., 2021; Short et al., 2021). Studies of large mammals found that communities containing species with higher tooth crown heights inhabit drier environments (Eronen et al., 2010b, 2010c; Fortelius et al., 2016; Fortelius et al., 2014; Short et al., 2021). However, recent work found that hypsodonty in North American small mammal communities is associated with mean annual temperature in addition to precipitation (Schap et al., 2021). Africa contains highly diverse, abundant, and unique small mammal communities, with 95% of the rodent species found in Africa being endemic to the continent (Kingdon, 2014). With a deep and rich evolutionary history, across many extreme climatic regions not found in North America (Bigalke, 1968), Africa is an ideal location to expand on previous work.

Rodents and Lagomorphs, or Glires, are an ideal study group for ecometric analyses because they can respond *in situ* to environmental changes (Badgley et al., 2014; Badgley and Finarelli, 2013; Montuire et al., 2006). These groups have high abundances in modern and fossil communities, small home ranges, limited dispersal ability (Bowman et al., 2002; Sandel et al., 2011; Schloss et al., 2012; Tucker et al., 2014), and relatively short life spans (Badgley et al., 2014; Badgley and Finarelli, 2013; Samuels and Hopkins, 2017; Schap et al., 2021). These life history characteristics are beneficial to ecometric studies because they allow for a more localized relationship between trait development and environmental changes as well as decreased lag time between environmental change and trait change when examining these relationships in deep time (Samuels and Hopkins, 2017). Despite these advantages, small mammals are still a relatively underutilized group when it comes to ecometric analyses and offer opportunities to supplement large mammal findings and expand the use of these methods to localities depauperate of large mammals.

Here, we first test if the ecometric relationships between hypsodonty and climate found in small mammals (Schap et al., 2021) persist in African communities. It is expected that the trait environment relationship of African small mammal communities will behave similarly to those in North America, as has been found with trait environment relationships of large mammals globally (Eronen et al., 2010b; Faith et al., 2020; Fortelius et al., 2016; Fortelius et al., 2002; Short et al., 2023; Žliobaitė et al., 2018), and will be characterized by communities with higher crown heights occurring in areas with colder and drier environments and communities dominated by lower crown taxa living in warmer and wetter environments. We then apply these relationships to the fossil record of eastern Africa, which hosts numerous well-studied fossil sites, to highlight the utility of ecometrics in temporal analyses at a singular site through time and spatial analyses comparing paleoclimate estimates across the landscape at contemporaneous fossil sites at various time periods over the last six million years. Lastly, we examine the community trait composition of the fossil communities and compare those to modern communities found at those localities today to understand the magnitude and direction of change in trait composition through time.

## 2. Materials and methods

### 2.1. Generating modern community data

We first compiled spatial data. The range maps of all African Glires species were generated from the IUCN Red List (IUCN Red List of Threatened Species, 2023). Next, modern climate variables including mean annual temperature (°C) and annual precipitation (mm) were gathered from the WorldClim Database at 0.5 × 0.5-degree resolution (Fick and Hijmans, 2017). Climate variables were transformed to be normally distributed by cubing mean annual temperature and logging annual precipitation. A 50-km equidistant point grid was overlaid across Africa (Lawing et al., 2012; Polly, 2010; Short et al., 2021; Short and Lawing, 2021) ($n = 12{,}046$). Species range maps and climate layers were sampled at each grid point to generate a dataset of small mammal communities with corresponding climate data.

We also compiled hypsodonty data for 94 (88%) modern African Glires genera (Table S1). To do so, we assembled published data on small mammal hypsodonty ($n = 87$), and additional specimens were measured from museum collections (the University of California Museum of Paleontology (UCMP) = 18 specimens across 14 genera; Texas A&M Biodiversity Research and Teaching Collections = 2 specimens across 2 genera; and Nairobi National Museum (KNM) = 5 specimens across 2 genera). If any taxa with published data were available to be measured at museums, those taxa were still measured to add confidence to their designation.

A Hypsodonty Index (HI) was calculated following methods from Janis (1988) and Fortelius et al. (2002) where hypsodonty is measured as a ratio of the unworn molar crown height divided by the occlusal width (Janis, 1988) or length of the same tooth (Fortelius et al., 2002; Van Valen, 1960). For museum specimens measured for this study, HI was calculated using the lower second molar (m2) following Fortelius et al. (2002). Based on the HI, teeth were placed categorically into brachydont, low crown teeth, with an HI < 0.8; mesodont being 0.8 < HI < 1.2; or hypsodont, high crown teeth, with an HI > 1.2 (Fortelius et al., 2002). For analyses, HI was ordinated so that brachydont taxa were given a value of 1, mesodont taxa a value of 2, and hypsodont taxa a value of 3. Some rodents and lagomorphs have ever-growing teeth, hypselodont, which in this study are grouped with hypsodont taxa following Fortelius et al. (2002) and Short et al. (2021). To determine the relationship between hypsodonty and climate, each taxon in a community was represented by the ordinated value of its tooth crown height. Then, a community-level trait value was generated by calculating the mean and standard deviation of the community hypsodonty (Fig. 1b).

Previous ecometric studies using large mammals, including carnivores or ungulates, have run analyses on communities consisting of three or more taxa (Short et al., 2023; Short and Lawing, 2021). There are a greater number of small mammal taxa present in and across communities so we increased our community size to five or more taxa (Short et al., 2021). We ran linear models of community mean hypsodonty against climate and found negligible differences between communities with a minimum of three species and those with a minimum of five species (Table S2, Fig. S1). For the remaining analyses, we report on communities with five or more taxa, resulting in 10,374 communities. We did not correct for phylogeny because it has been found that the ecometric relationship is not sensitive to phylogenetic differences between communities (Lawing et al., 2017; Polly et al., 2017; Short and Lawing, 2021). All analyses were conducted in RStudio (R Core Team, 2023).

### 2.2. Modern analyses

We initially visualized our data using scatterplots of hypsodonty

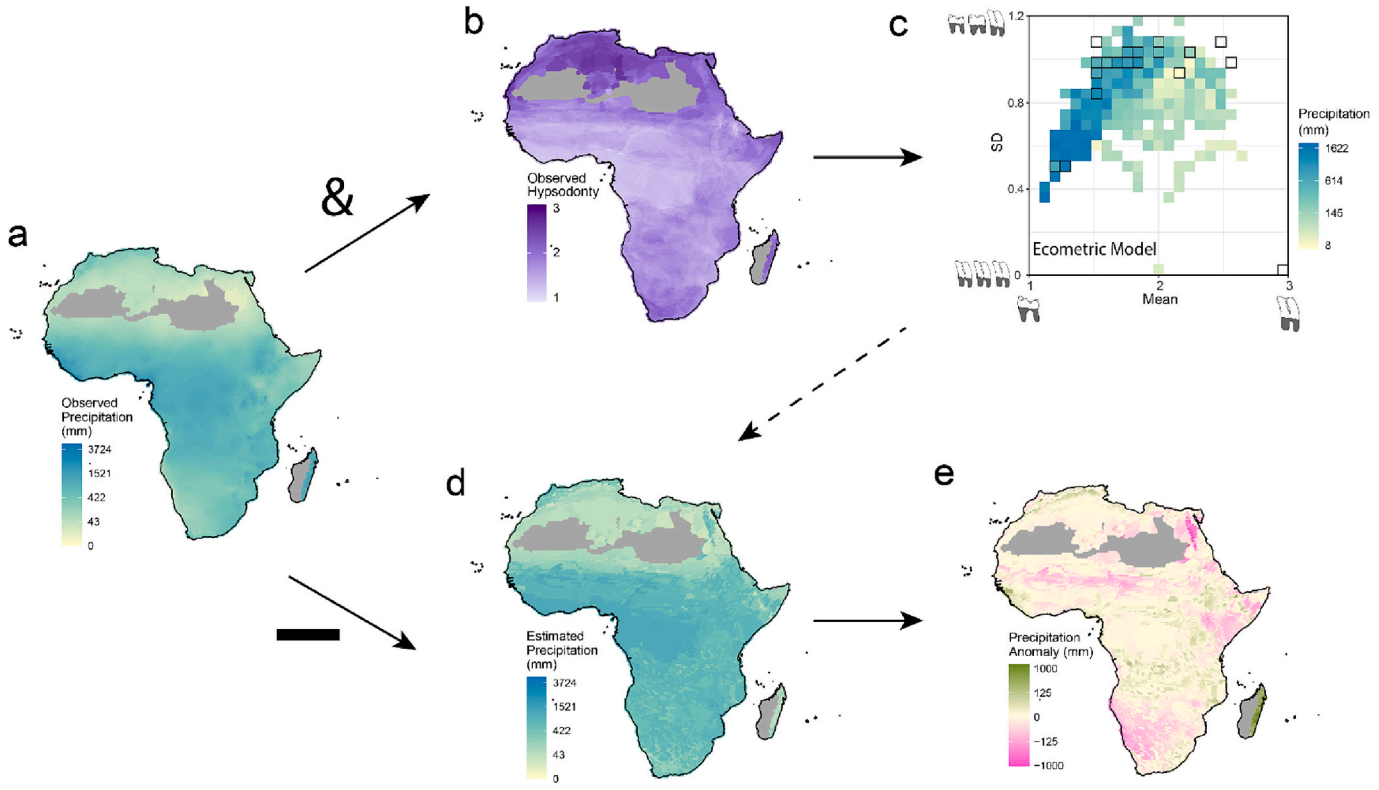


**Fig. 1.** Ecometric model inputs and outputs. (a) Observed precipitation and (b) observed hypsodonty data are used to generate (c) the ecometric model, shown as an ecometric trait space, which shows the maximum likelihood annual precipitation values for all communities with a given mean and standard deviation crown height. The ecometric model is projected onto Africa to generate (d) an estimated precipitation map. (a) Observed precipitation minus (d) the estimated precipitation gives (e) the precipitation anomaly. Black boxes on the ecometric trait space represent bins where fossil sites were placed.

versus annual precipitation and mean annual temperature. Linear models were then used for variable selection and to approximate the variance explained for each climate variable (Table S2, Fig. S1). Linear models showed there was not a strong relationship between community-level mean hypsodonty and mean annual temperature (Fig. S1, Table S2 $y = -5457\times + 23{,}655$, $r^2 = 0.09$, $r = -0.30$, $p < 0.001$). However, there was a strong relationship between community-level mean hypsodonty and annual precipitation (Fig. S1, Table S2, $y = -15.7\times + 43.3$, $r^2 = 0.61$, $r = -0.78$, $p < 0.001$), so further analyses focus only on annual precipitation. A functional relationship between hypsodonty and aridity is clear and established, resulting from ingested grit. However, in diverse landscapes and among taxa with diverse dietary habits, there will often be diversity in the hypsodonty exhibited by different species. This can be captured by the standard deviation of the community.

An ecometric model was constructed using a maximum likelihood approach. We first binned communities into a 25 × 25 matrix based on the mean and standard deviation of their community hypsodonty (Fig. 1c) (Lawing et al., 2012; Short and Lawing, 2021; Vermillion et al., 2018). For each bin, we estimated a probability density function using kernel density estimation with a Gaussian smoothing kernel, and the precipitation value where the curve was at its maximum is the most likely annual precipitation value, following Short and Lawing (2021) and Vermillion et al. (2018). We assessed the transferability of our model through a sensitivity analysis (Fig. S2) (Short et al., 2023). We randomly down-sampled our 10,374 communities ranging from 100 to 9100 communities at intervals of 1000. The randomly down-sampled community was iterated 20 times for each sample size. Every iteration of every sample size was divided so that 80% of the data was used as training data for the model and the remaining 20% was used to test the model.

To assess how well our ecometric model estimates precipitation, we calculated anomaly maps (Fig. 1e), which identify the environments where our model estimated annual precipitation well and the environments where the model did not. Maps of estimated precipitation were generated using the maximum likelihood estimates based on community hypsodonty values and the ecometric model (Fig. 1d). Anomaly maps display the differences between the estimated precipitation maps (Fig. 1d) and the observed precipitation maps from WorldClim (Fig. 1a) (Fick and Hijmans, 2017; Short and Lawing, 2021; Vermillion et al., 2018). As anomaly maps depict the difference between observed climate and estimated climate, areas where the model overestimates will have a negative anomaly value while areas where climate is underestimated will have a positive anomaly value (Fig. 1e).

### 2.3. Generating Fossil Community Data

Once the modern relationship was established, we created a list of fossil localities in eastern Africa where we could estimate paleoprecipitation (Fig. 3; Table S3). Some taxa at these sites are extinct and not included in our dataset of modern taxa. Data for three extinct taxa were collected from the literature. Taxa not available in the literature were measured from specimens in museum collections (UCMP = 3 specimens across 2 genera; National Museum of Kenya (NMK) = 8 specimens across 4 genera). Overall, hypsodonty data for 9 extinct genera were collected (Table S1). Taxa were placed into brachydont, mesodont, or hypsodont following the methods used for modern taxa. As the linear models of modern correlations between hypsodonty and annual precipitation in communities of three or more taxa and five or more taxa showed negligible differences (Table S2), fossil localities with at least three taxa were used in our analyses resulting in 26 fossil sites across Kenya ($n = 10$), Ethiopia ($n = 11$), and Tanzania ($n = 6$) (Fig. 3; Tables S3, S4). One locality, Shungura, had four nonoverlapping stratigraphic layers spanning from 1.9 Ma to 3.44 Ma that allowed for the examination of changes in the precipitation levels at one locality through time.

### 2.4. Fossil analyses

Fossil communities were analyzed using our ecometric model, based on the mean and standard deviation of their community mean crown height (Fig. 1c). Paleoprecipitation estimates for each site were produced from the maximum likelihood annual precipitation value of the trait bin in which the site fit. Confidence intervals for precipitation values were calculated at the 5% limits on either side of the maximum value of the Gaussian curve for each community's assigned ecometric bin. We then utilize our fossil sites to highlight the variety of ways ecometrics can contribute to paleoecology. First, we compared changes in precipitation and community trait means in one location through the four well-sampled microfauna layers from Shungura Members B, C, F, and G (Fig. 2a). We also examined the heterogeneity of precipitation on a spatial scale by grouping our fossil sites into Late Miocene (6.12–5.7 Ma), Pliocene (4.5–2.5 Ma), and Early Pleistocene (2.36–1.2 Ma) time bins and comparing the estimated precipitation at contemporaneous sites located across eastern Africa (Fig. 3). Finally, we compared modern communities to those of the past to show the direction and magnitude of change through time. To do this, we gathered modern precipitation from a sampling point nearest to each of the fossil sites and examined these modern communities alongside the fossil communities in trait space (Fig. 2b).

## 3. Results

### 3.1. Modern Relationships

Our ecometric model, visually depicted as an ecometric trait space (Figs. 1c), reveals an overall trend of higher precipitation values for communities with lower tooth crown heights, with means between 1 and 2, and lower precipitation values for communities with higher mean tooth crown heights between approximately 2 and 2.5. No communities had a mean tooth crown height of 3. The standard deviation of community-level tooth crown height ranged from 0.4 to 1.2 but did not have a clear relationship with precipitation in trait space. With a sensitivity analysis, we found that the correlations between crown height and precipitation of the testing data stabilized at 0.76 around a sample of 2500 communities (Fig. S2). For the testing data, residuals between our observed precipitation and estimated precipitation, often referred to as anomalies in ecometrics, stabilized around 3 log mm with a sample of 2500 communities. Our ecometrics model was run using all 10,374 communities, which is well above the number of communities needed according to our sensitivity analysis to accurately capture the trait-environment relationship between crown height and precipitation.

Our maps of estimated precipitation encompass most of Africa except where there are no communities with at least 5 small mammal taxa available, such as the Sahara Desert and Madagascar (Fig. 1a). Estimated precipitation (Fig. 1d) closely follows trends seen in observed precipitation (Fig. 1a) with lower precipitation values across the northern region associated with higher community mean hypsodonty (Fig. 1b) and high precipitation values in the central region associated with lower community mean hypsodonty (Fig. 1b). Observed precipitation from climate data and estimated precipitation from the ecometric model have a strong positive relationship ($y = 0.7887\times + 4.11$, $r^2 = 0.68$, $r = 0.83$, $P < 0.001$) (Fig. S4).

Anomalies, or residuals, are relatively low across Africa (Fig. 1e), indicating the model estimates have high accuracy. Negative anomalies are more frequent than positive anomalies (Fig. S3). Areas with positive anomaly values, or where precipitation was underestimated, are mostly in northern coastal regions, the central region, and along the east coast of Madagascar. Areas with negative anomalies, or where precipitation was overestimated, are in the Nubian Desert, the border of the Sahara Desert and the Sahel, the Namib and Kalahari Deserts, and east of the Great Rift Valley (Fig. 1e).

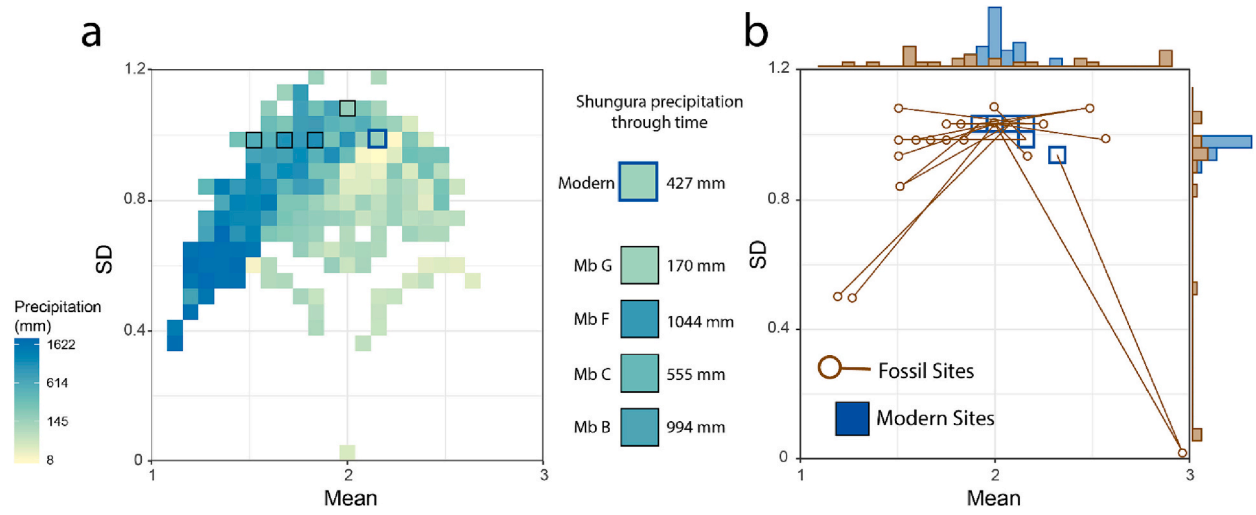


**Fig. 2.** (a) The eometric model. The four fossil layers of the Shungura site are represented by black boxes around their trait bin and the modern trait bin for Shungura is represented by a dark blue box. (Center) Shifts in precipitation values at Shungura with the layers being stacked stratigraphically from the oldest layer (Mb B) at the bottom and modern precipitation at the top. (b) A comparison of modern and past trait spaces. All fossil site trait bins are represented by an open brown circle with a brown line extending towards the modern trait space for that locality. We can see homogenization of the fossil sites onto six modern trait bins. Histograms on the x and y axes show the distribution of modern and fossil sites with a given mean and standard deviation of tooth crown height. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

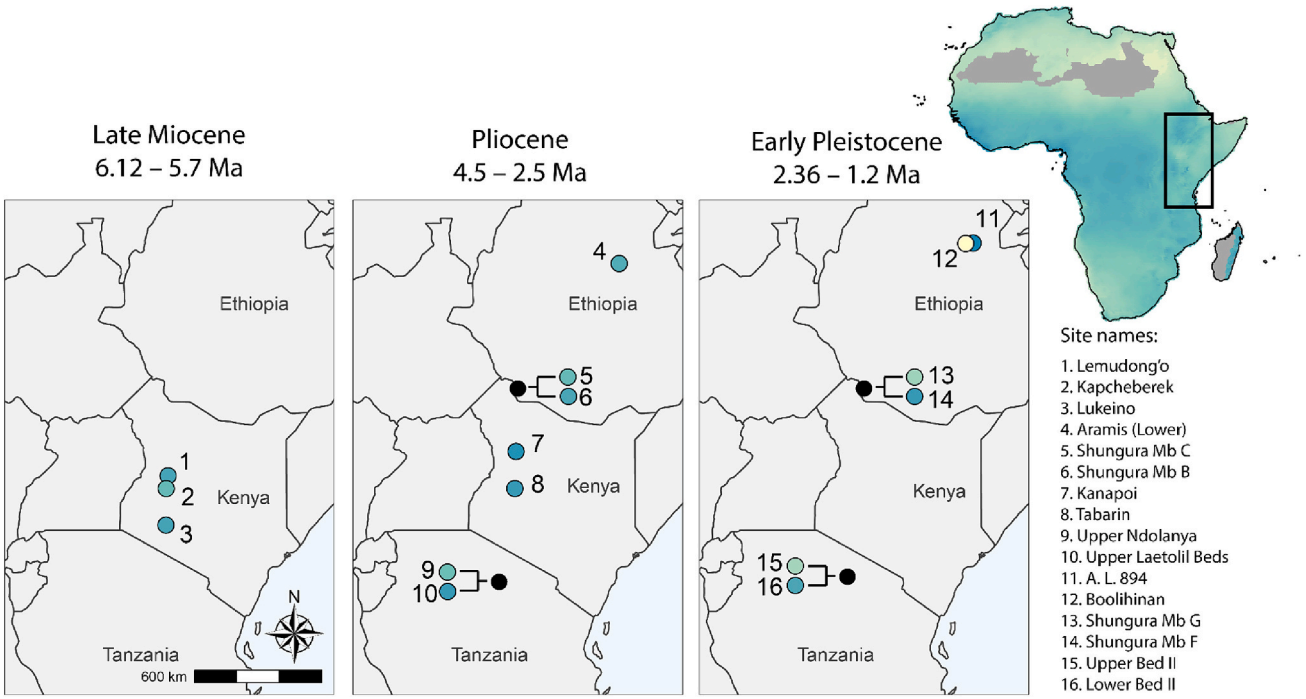


**Fig. 3.** All fossil localities grouped based on geologic time, with Late Miocene sites on the left, Pliocene sites in the middle, and Early Pleistocene sites on the right, showing spatial heterogeneity of precipitation through time regardless of proximity between sites. Sites with more than one layer in a given time period are represented by a black dot that branches out to show the two layers lined up stratigraphically. The color of the circle corresponds with the precipitation value using the legend in Fig. 3, with yellows being drier and blues being wetter.

### *3.2. Fossil Site estimates*

The 26 fossil sites are associated with 19 eometric trait bins, and modern communities from the geographic locations of each fossil site are associated with 6 bins, illustrating homogenization into the modern (Fig. 2b). Fossil sites have a range of mean crown heights from 1.25 to 3.00 and standard deviations of 0–1.15. Modern communities have a range of 1.91 to 2.31 and a standard deviation of 0.85–0.95 (Fig. 2b). Of the 26 fossil localities, we report estimated paleoprecipitation values for 16 of them (Table S4). The other 10 sites have community hypsodonty mean and standard deviation values outside of the modern trait space, and therefore, we cannot estimate the annual precipitation at those sites using the eometric model (Fig. 1b). Most fossil localities with paleoprecipitation estimates have high estimated precipitation values, hypsodonty means of two or less, and hypsodonty standard deviations between 0.5 and 1 (Fig. 1c, Table S4). Fossil localities where paleoprecipitation estimates are not available typically have high mean crown heights of two or more and a bimodal distribution of standard

deviations of zero or over one. Fossil sites occur in bins with precipitation estimates ranging between 5 and 1617 mm whereas the modern communities occur in bins that are generally drier with precipitation estimates ranging between 302 and 599 mm.

Temporally, we examine estimated annual precipitation values for the four stratigraphic layers preserved at Shungura. Estimated precipitation decreases from 994 mm at Member B, the oldest layer, to 555 mm at Member C, then increases to 1044 mm at Member F, and greatly decreases to 170 mm at Member G, the youngest layer (Fig. 2a). Spatially, we investigate fossil sites across East Africa in three time bins. The Late Miocene time bin contains the Lemudongo, Kapcheberek, and Lukeino fossil localities from Kenya, and estimated annual precipitation values range from 480 mm at the central Kapcheberek to 824 mm at the northern Lemundongo. The Pliocene time bin contains Aramis (lower), Shungura Members B and C, Kanapoi, Tabarin, Upper Ndolanya, and the Upper Laetolil Beds across Ethiopia, Kenya, and Tanzania with estimated annual precipitation ranging from 404 mm at the southern Upper Ndolanya to 1127 mm at the central Kanapoi. The Early Pleistocene time bin contains A.L. 894, Boolihinan, Shungura Members F and G, Upper Bed II, and Lower Bed II across Ethiopia and Tanzania with estimated annual precipitation values ranging from 5 mm at the northern Boolihinan to 1583 mm at A.L. 894, which is geographically similar to Boolihinan (Fig. 3).

## 4. Discussion

### 4.1. Modern relationships

Examination of the ecometric relationship between small mammal hypsodonty and climate revealed different results from the previous North American study. Similarly to North America (Schap et al., 2021), there was a strong relationship with annual precipitation. However, unlike in North America (Schap et al., 2021), there was no relationship found between community-level hypsodonty and mean annual temperature in Africa (Fig. S1). We suggest the continental discrepancies between the relationship with mean annual temperature and hypsodonty are due to less variation in mean annual temperature across Africa (95% CI: 15.7 to 29.2 °C) compared to North America (95% CI: −19.0 to 23.9 °C). In contrast, the stronger relationship between community-level hypsodonty and annual precipitation could be because annual precipitation varies more widely across Africa (95% CI: 3 to 1954 mm) than in North America (95% CI: 115 to 1802 mm), and Africa has more variation in precipitation seasonality (95% CI: 26.7 mm to 161.8 mm) compared to North America (95% CI: 13.7 to 95.5 mm).

Taxa in Africa could be less constrained by temperature but rather, would need to be adapted to changes in precipitation during the dry season. The timing of rainfall is important to primary productivity and vegetation types, and it contributes to the crown height of the community (Janis et al., 2004). Dust and grit settling on vegetation during the dry season would necessitate more hypsodont dentition in a community whereas those communities in environments with adequate precipitation, even in the dry season would be more prone to less hypsodont dentition. Small mammals, with limited dispersal ability, show morphological adaptations in response to changing climate rather than community reassembly through dispersal (Bowman et al., 2002; Heikinheimo et al., 2007; Samuels and Hopkins, 2017). With the majority of the small mammal taxa in Africa being endemic specialized taxa, it could explain why the relationship between community-level crown height and annual precipitation was so strong as small mammals are uniquely suited to their particular environment.

Of the taxa we were able to gather hypsodonty data for, an almost equal number of brachydont ($n = 41$) and hypsodont ($n = 37$) taxa were found across Africa while there are roughly half the number of mesodont taxa ($n = 17$). Many brachydont (= 1) and hypsodont (= 3) taxa produce means of 2 but create a wide range in standard deviation (Fig. 2c). The North American study found that the percent of brachydont taxa and the number of hypselodont taxa within a community were two of the most important variables in building regression equations of climate (Schap et al., 2021) and attributed that to these taxa being more specialized for particular climates and environments.

Anomalies are highest in the wettest and the driest areas, as is seen across ecometric studies (Schap et al., 2021; Short et al., 2023; Short et al., 2021; Short and Lawing, 2021; Vermillion et al., 2018), due to our maximum likelihood method that takes the most likely climate value for a given trait bin to estimate climate for all communities within that trait bin. Anomaly maps from North America found the highest anomalies along elevational gradients, like the Rocky Mountains, and along the coasts (Schap et al., 2021). In Africa, the Turkana basin between the East African Dome and Ethiopian Dome has a high negative anomaly, possibly because of the area's complex topography. Some mountainous areas, like the Atlas Mountains, had highly positive anomalies. Highly negative anomalies were found mostly in deserts, including the Sahara, Kalahari, Ogaden, and Namib, and in areas of transitional precipitation, for example, in the Sahel between the Sahara Desert and the Congo Basin (Fig. 1e). Taxa in the Sahel are largely brachydont (Fig. 1b) and are having to adapt to an area that has experienced prolonged drought brought on by increased anthropogenic impacts like overgrazing, converting woodland to agriculture, and large scale atmospheric circulation changes (Zeng, 2003); perhaps the taxa found in the Sahel region are too specialized in their tooth crown heights to accurately estimate precipitation.

### 4.2. Fossil relationships

Application of our model to fossil localities adds additional information to previous interpretations of local environments and biota across time and space. For example, we highlight trends in precipitation and community crown height in relation to the presence or absence of lakes in the East African Rift System (EARS) and local rivers through time. At Olduvai Basin, we illustrate effects of deep freshwater lakes during intensification of the Walker Circulation (Trauth et al., 2007). Our model generates a high precipitation estimate of 1127 mm at Lower Bed II, which has a mean hypsodonty of 1.5, from 1.79 to 1.74 Ma followed by a decrease in estimated precipitation to only 149 mm at Upper Bed II from 1.74 to 1.2 Ma, corresponding with the drying up of the Olduvai paleolake and an increase in mean hypsodonty to 2.25 (Kovarovic et al., 2013; Maslin et al., 2014; Trauth et al., 2007; Trauth et al., 2005) (Table S4).

We also track shifting precipitation patterns at one site over approximately 1.5 Ma at the well-dated and well-sampled Shungura Formation (Fig. 2a) (Bibi et al., 2013; Boisserie et al., 2008; Levin et al., 2011; Plummer et al., 2015). Member B, with an estimated annual precipitation of 994 mm from our models, aligns with periods of large deep lakes in the area as well as the presence of a river (Maslin et al., 2014; Trauth et al., 2007; Trauth et al., 2005; Wesselman, 1984). Member C, with a decrease in estimated annual precipitation to 555 mm, spans a period of increasing aridity with no paleolakes and no local river (Bibi et al., 2013; Maslin et al., 2014; Trauth et al., 2007; Trauth et al., 2005). Member F, with an estimated annual precipitation of 1044 mm, does not fall within the presence of paleolakes in eastern Africa but does have a local river nearby, confirming the presence of surface water associated with higher precipitation (Maslin et al., 2014; Trauth et al., 2007, Trauth et al., 2005; Wesselman, 1984). Member G, with an estimated annual precipitation of 170 mm is not associated with a river environment but does fall during the presence of shallow lakes in the EARS (Maslin et al., 2014; Plummer et al., 2015; Trauth et al., 2007; Trauth et al., 2005). The low level of precipitation estimated by high hypsodonty (Table S4) at Member G reflects the expansion of edaphic grasslands (Table S3) (Plummer et al., 2015). This suggests that shallow lakes in the EARS, rather than widespread deep lakes, are not a strong enough influence to alter community trait composition.

Shungura is a useful example to point out the complexities in trait-

environment relationships as a proxy for past climate. While the small mammal taxa responded to changes in their local environment, their local environment, namely the vegetation they consume, in the Turkana Basin was influenced by hydrological events happening hundreds of kilometers away in the Ethiopian Highlands (Maslin et al., 2014; Trauth et al., 2007, Trauth et al., 2005). This mismatch of scale is also seen at sites where there has been regional volcanic activity generating abrasive ash that covered the landscape and altered climate patterns, such as in the Columbia River Valley during the Middle Miocene (Kürschner et al., 2008; Retallack, 2007; Zachos et al., 2001) and in the Ethiopian Rift at 45–33 Ma (Trauth et al., 2007, Trauth et al., 2005). Hypsodonty might also reflect water availability in the local environment rather than just the amount of precipitation itself. The hydrological and geological context of fossil sites allows us to identify other factors that might be influence the relationship between hypsodonty and precipitation.

Eastern African climate has long been understood to be variable across landscapes and punctuated by periods of increased drought and aridity or increased temperatures (Bobe, 2006b; Lukich and Ecker, 2022; Maslin et al., 2014). This is evident at fossil sites through the Pliocene ranging from oldest to youngest: 830 mm at Tabarin, 666 mm in Aramis (Lower), 1127 mm in Kanapoi, 1044 mm in Upper Laetolil Beds, 994 mm at Shungura Member B, 404 mm at Upper Ndolanya, and 555 mm at Shungura Member C (Fig. 3; Table S4). Similar fluctuations through time are seen at our Early Pleistocene sites from Tanzania to Ethiopia (Fig. 3; Table S4). Even today, rainfall in eastern Africa is largely influenced by inter-annual variability caused by large-scale climate forcing and changes in sea surface temperatures leading to droughts and floods (Gebrechorkos et al., 2019; Niang et al., 2014). However, with ecometrics, we are able to highlight some paleoclimate trends, such as increasing aridity and decreasing annual precipitation from 824 mm to 480 mm in the Late Miocene of Kenya, mirroring what has been found from other regions of the continent (Bobe, 2006b; Jacobs, 2004).

Fossil communities were often dominated by low-crowned brachydont taxa with few hypsodont taxa found at these sites in the past (Table S3). An exception is Upper Ndolanya, which has the highest mean tooth crown height recorded until that time at 2.66 Ma with a subsequent decrease until 2.33–1.9 Ma at Shungura Mb G. Upper Ndolanya has been described as semi-arid scrub or bushland (Kovarovic et al., 2002) and corresponds with Ngorongoro volcanism (Maslin et al., 2014; Trauth et al., 2005). Volcanism leads to selection for higher crown taxa as they can better withstand an increase in ash and grit in their diet.

Modern communities at fossil localities are more evenly split between high-crowned and low-crowned taxa, causing mean community trait values to average around 2.0 with standard deviation near 1.0. Homogenization of mean hypsodonty across small mammal communities in eastern Africa is consistent with previous studies of other functional traits and taxa (Short and Lawing, 2021; Tóth et al., 2014). Africa has many endemic taxa that are highly specialized to their environments (Bigalke, 1968; Cloudsley-Thompson, 1989; Heslop-Harrison, 2011) and our communities are therefore composed of many specialist taxa driving standard deviation changes. Overall, an increase in the modern presence of hypsodont taxa generates lower precipitation estimates than were seen in the past. Decreasing precipitation across eastern Africa into the modern has also been found over the last 6 million years from the Turkana Basin using hypsodonty and loph count of large mammals (Fortelius et al., 2016).

One shortcoming of our ecometric analysis is that we are only able to generate paleoprecipitation for communities with trait compositions found in modern communities. Ten of the fossil sites were composed of non-analog trait compositions that were not represented in our modern ecometric model, meaning we could not generate paleoprecipitation estimates for those sites. With an expected increase in no-analog communities as species reassemble in response to changing climates (Hobbs et al., 2018), perhaps some of these fossil communities will have the same trait values as future communities. Future work should incorporate the presence of non-analog communities from the past because these will be increasingly important for understanding heightened variation in modern communities.

## 5. Conclusions

These results help expand upon the use of ecometrics in small mammal communities and aid in understanding global relationships between fauna and their environment. We also show that ecometrics is a useful and easily applied method that allows us to quantitatively study climate trends from a wide range of fossil sites both spatially and temporally. While some fossil sites have paleoclimate reported from local or regional proxies, no single proxy has been applied easily and cost-effectively to compare past climate across multiple fossil sites. Paleoclimate estimates generated from our model can be applied to any African fossil site where there are at least 3 small mammal taxa present and can be useful at sites where pollen or isotope data may not be available. Our estimates can also help to add more nuance to previously described sites and highlight how the fauna themselves are influenced by climate. Over the last six million years, the small mammal fauna has been highly specialized to their local environments. As climate change continues to reshape what our modern landscapes and climates look like, the strong modern trait-environment relationships of these specialized communities may begin to weaken, as we are already seeing in areas like the Sahel. Future directions of this work should examine whether these specialized taxa are in danger given future expected climate, or if they will continue to adapt or move quickly enough to maintain a stable trait-environment relationship.

## Funding sources

This work was completed as part of a collaborative initiative from NSFDEB-NERC, with funding from [NSF # 2124836] to A.M.L., F.K.M., and J.L.M.; [NSF # 2124770] to J.L.M.; [NSF-CAREER, NSF #1945013] to J.L.M. which also helped fund J.A.S; and United States Department of Agriculture National Institute of Food and Agriculture Multistate project [# 7004187] to R.A.S.

## CRediT authorship contribution statement

**Julia A. Schap:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jenny L. McGuire:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization. **A. Michelle Lawing:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Fredrick K. Manthi:** Writing – review & editing, Writing – original draft, Visualization, Resources, Funding acquisition, Data curation, Conceptualization. **Rachel A. Short:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

All analyses were performed in the R Computing Environment (R Core Team, 2023) and are available on figshare (https://doi.org/10.6084/m9.figshare.24757578 (Schap et al., 2023); for peer-

review: https://figshare.com/s/431cf676f8b361f2c4ad).

## Acknowledgements

We would like to thank the Spatial Ecology and Paleontology Lab at Georgia Tech for their helpful insights throughout the research process, especially Benjamin Shipley for his help with modern faunal lists for African small mammals as well as helping to calculate the range in MAT, AP, and precipitation seasonality for Africa and North America. We would also like to thank Drs. Chris Conroy and Patricia Holroyd from The Museum of Vertebrate Zoology (MVZ) and University of California Museum of Paleontology (UCMP) respectively, Jessica Light from the Biodiversity Research and Teaching Collections at Texas A&M, and Jimmy Yatich and Rose Kavurani from the Nairobi National Museum for their assistance in providing access to specimens used in this study and María Alejandra Hurtado Materon for providing measurements of specimens from Texas A&M and the Nairobi National Museum. Lastly, we would like to thank Dr. Jason Head for his work as a co-PI and Dr. Johannes Müller for his intellectual contributions on the NSF # 2124836 grant.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2024.112181.

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