PNAS RESEARCH ARTICLE | ECOLOGY

The utility of body size as a functional trait to link the past and present in a diverse reptile clade

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Edited by Nils Stenseth, Universitetet i Oslo, Oslo, Norway; received March 16, 2022; accepted August 30, 2022

Understanding the relationships between functional traits and environment is increasingly important for assessing ecosystem health and forecasting biotic responses to future environmental change. Taxon-free analyses of functional traits (ecometrics) allow for testing the performance of such traits through time, utilizing both the fossil record and paleoenvironmental proxies. Here, we test the role of body size as a functional trait with respect to climate, using turtles as a model system. We examine the influence of mass-specific metabolic rate as a functional factor in the sorting of body size with environmental temperature and investigate the utility of community body size composition as an ecometric correlated to climate variables. We then apply our results to the fossil record of the Plio-Pleistocene Shungura Formation in Ethiopia. Results show that turtle body sizes scale with mass-specific metabolic rate for larger taxa, but not for the majority of species, indicating that metabolism is not a primary driver of size. Body size ecometrics have stronger predictive power at continental than at global scales, but without a single, dominant predictive functional relationship. Application of ecometrics to the Shungura fossil record suggests that turtle paleocommunity ecometrics coarsely track independent paleoclimate estimates at local scales. We hypothesize that both human disruption and biotic interactions limit the ecometric fit of size to climate in this clade. Nonetheless, examination of the consistency of trait–environment relationships through deep and shallow time provides a means for testing anthropogenic influences on ecosystems.

conservation | paleobiology | ecometrics | reptiles

Significance

Functional traits are important for forecasting biotic response to climate change. However, the fit of traits to environment is often poorly understood across habits and habitats. We test the functional relationship of body size to climate and the role of metabolism in governing size in turtles. Complex relationships between size and environment in modern turtles suggest that temperature-dependent metabolism is not a primary functional driver of maximum size and that human impacts and other biotic interactions have disrupted modern turtle body size distributions. Using modern trait–environment relationships to estimate paleoenvironments in the fossil record can coarsely predict paleoclimate. Further inclusion of fossil data to examine functional traits may improve the ability to assess and forecast future responses.

In healthy ecosystems, the distributions of functional traits should be sorted by environmental relationships (1–3) and are, therefore, important for conservation forecasting and response strategies (4–7). Trait–environmental relationships can be modeled across a range of communities and habitats, and the resultant models can be applied to future climate change projections to forecast expected trait distributions for communities adapted to particular future climatic conditions. Such distributions can then be used to identify which species are at risk for extirpation or extinction because their traits do not fall within the projected community distribution and, conversely, which species' traits will be well suited for future climates.

Key to utilizing traits is an understanding of the functional factors that govern performance. Hypotheses of trait function are determined through direct behavioral observation, experimental mechanistic approaches, or spatial correlation of trait distributions with environmental variables (8) with post hoc inference of functional relationships (9). The development of taxon-free analysis of functional traits (ecometrics) allows further tests of function across clades and through time (9–12). Application of modern ecometric models to trait distributions in fossil communities (hindcasting) allows us to evaluate histories of niche stability (13, 14). Comparing estimates from hindcasting to independent coeval paleoclimate proxies can provide data on trait resilience or shifts in functional factors over time, which should be established in order to use ecometric models to forecast community compositions in response to future climate change (11). Here we examine the utility of body size as an environmentally correlated functional trait in extant turtles, both in the context of metabolic scaling with temperature for species' size maxima and as a community ecometric correlated to temperature and precipitation. We apply our ecometric models to the fossil record of turtles from the Plio-Pleistocene eastern African tropics to assess whether modern ecometric relationships persist through time, and are therefore potentially useful for conservation planning.

Body size is an important functional trait for examining biotic responses to environmental change, with multiple functional factors sorting size, including metabolism, developmental rate, and changes in ecosystem structuring (15, 16). In poikilotherms, temperature-dependent metabolism has been proposed as a mechanism to explain either increases in body size with temperature for mass-specific metabolic rates or

Author contributions: A.K.P. and J.J.H. designed research; A.K.P. performed research; J.-R.B., A.K.P., J.J.H. and J.M. conducted field research; A.K.P. analyzed data; and A.K.P., J.M., J.-R.B., and J.J.H. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2201948119/-/DCSupplemental.

Published February 6, 2023.

decreases in size based on increasing growth and metabolism (16, 17). Disentangling the relative roles of metabolism and life history processes in driving trait distribution is crucial for understanding potential responses to critical climate maxima and trophic responses to trait shifts (18, 19).

Turtles are widely distributed and speciose (20) (Fig. 1*A*), and are a conservation concern, with over 50% of species classified as endangered due to habitat loss and human predation (21). Turtles are ecologically diverse, with habitats and habits ranging from fully terrestrial herbivores to obligately aquatic carnivores, and body sizes of extant species ranging from carapace lengths of 11 cm to 150 cm (Dataset S1). Previous analyses of body size distributions in extant taxa at a global scale have found positive correlations between size, latitude, geographic range, and temperature (22, 23), but have not found strong support for the functional factors underpinning these relationships. Analyses of within-lineage size trends have additionally found inverse relationships of body size to environmental temperature (24–26), further confounding functional inferences of the role of metabolism and the reliability of body size as a functional trait.

To determine whether turtle body size distributions are correlated to metabolic rate, we model expected maximum size for minimum mean annual temperature (MAT) within geographic ranges of aquatic and terrestrial species (*SI Appendix*) based on the size–MAT relationships for the largest living species, using a metabolic scaling model based on the Q_{10} coefficient which describes oxygen consumption changes per temperature change by 10 °C (17). We compare model predictions with actual size–temperature relationships for living species. To model size as a community ecometric, we apply linear regression (LR) and maximum likelihood (ML) models to determine the predictive power of turtle body size distributions for estimating climate variables including MAT and mean annual precipitation (MAP). We use standard ecometric approaches and, additionally, train ecometric models using range predictions for turtle species derived from species distribution models (SDMs). SDMs model geographic ranges where environmental conditions are for each species, which minimizes the effects of anthropogenic extirpation and habitat loss on estimating trait–environmental relationships. Comparisons of these models reveal which input datasets and spatial scales capture the strongest ecometric relationships.

We hindcasted modern ecometric and scaling relationships onto the turtle fossil record of the Plio-Pleistocene Shungura Formation of Ethiopia and compare results with other paleoclimate proxies to determine whether extant relationships are sufficient for predicting nonanalog climates of the past, and, by extension, the future. The Shungura Formation consists of fluviolacustrine sediments and intercalated volcanic tuffs cropping out west of the Omo River in southwestern Ethiopia (ref. 27 and references therein). It preserved a dense, well-sampled vertebrate fossil record representing both terrestrial and aquatic ecosystems, including a diversity of turtles (Fig. 1*B*), as well as paleoclimate estimates from paleobotanical, faunal, and geochemical proxy data (28–33). The Shungura Formation is precisely chronostratigraphically dated throughout from ∼3.6 Ma to 1.0 Ma, and thus records faunal responses of rich tropical vertebrate communities to climate parameters equivalent to projections of future anthropogenically mediated warming (34). As a result, it represents an excellent model system for testing functional traits beyond modern environments.

Results

Turtle Body Sizes Scale with Mass-Specific Metabolic Rate for Larger Taxa. For the majority of aquatic and terrestrial species, maximum body size is smaller than predicted by metabolic scaling, with numerous small-bodied taxa occurring in hot climates (Fig. 2 *A* and *B*). The anomaly between actual and modeled MAT is significantly inversely related to carapace length for both aquatic and terrestrial taxa, however (regression slopes range from −8.85 to −4.25, R^2 range from 0.18 to 0.67, $P < 0.0001$ for all models; *SI Appendix*), indicating a stronger relationship to metabolic scaling with increasing body size (*SI Appendix*, Fig. S2). Several large-bodied taxa occurred with colder-than-predicted MATs. These records suggest either that body sizes of *Chitra* or *Centrochelys* may not represent the possible maxima in modern climates or that Q_{10} rates are lower than two for some taxa at colder MATs.

Projecting body sizes of Shungura Formation turtles and MAT estimates from pedogenic carbonate isotope proxies (33) (*SI Appendix*, Table S2) into the model space for extant taxa reveals no metabolic size scaling in the Pleistocene eastern African

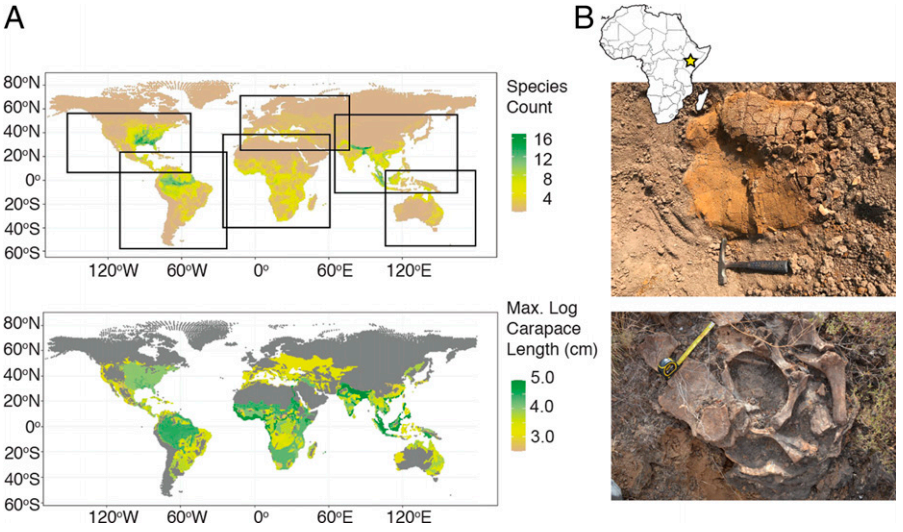

Fig. 1. (*A*) Geographic distributions of species richness (*Top*) and maximum body size, measured as carapace length (*Bottom*), for extant turtles. Rectangles denote ranges used for continental-scale ecometric analyses. (*B*) Turtle fossils from the Shungura Formation of Ethiopia (yellow star on *Inset* map). (*Top*) The aquatic trionychid turtle *Trionyx cf. triunguis*, carapace in dorsal view, rock hammer for scale, Member G. (*Bottom*) The terrestrial tortoise cf. *Centrochelys* sp., partial carapace, girdles, and appendicular skeleton in visceral view, with tape measure for scale, Member H.

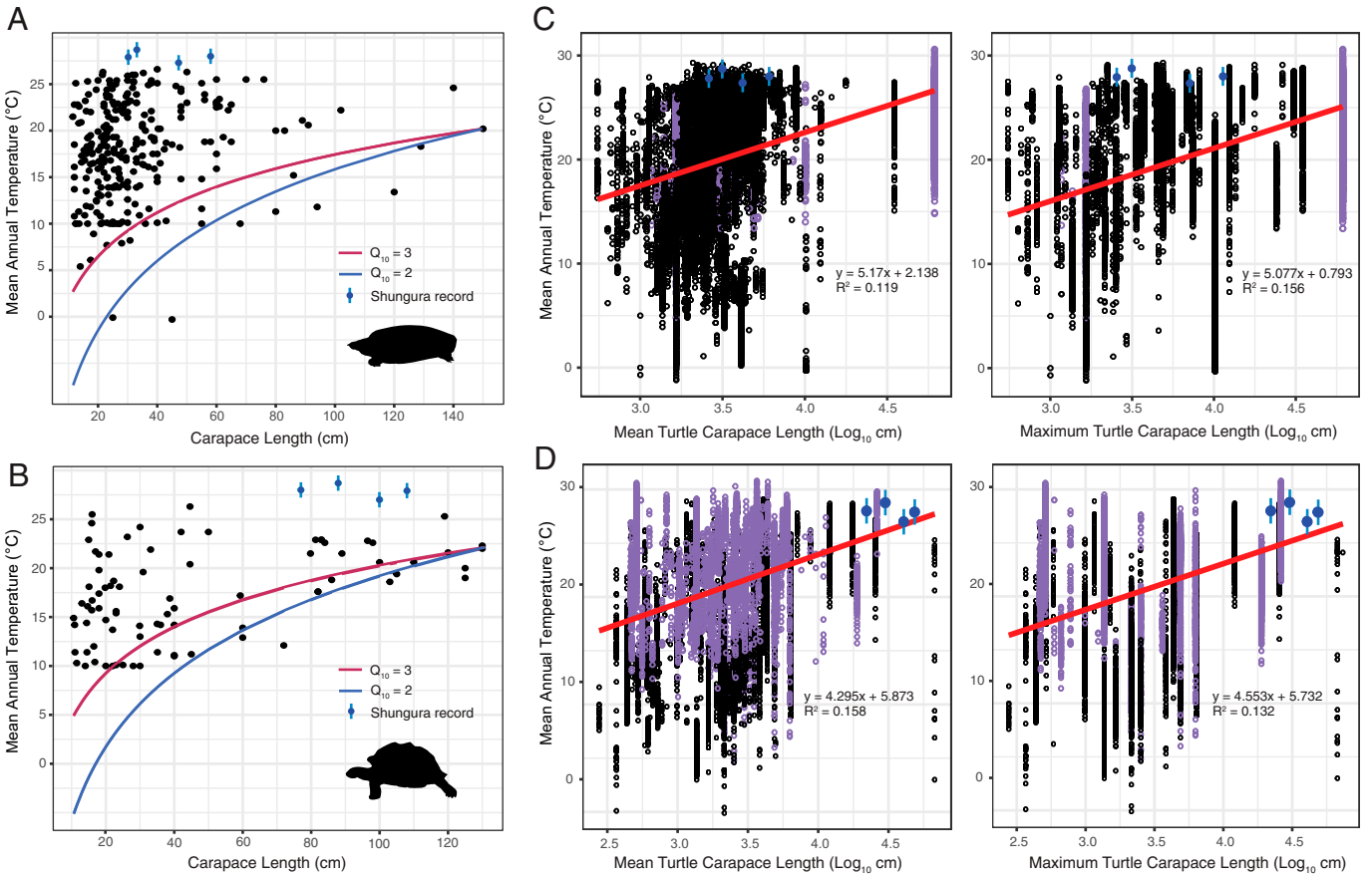

Fig. 2. (*A*) The model relationships between turtle body size and minimum MAT based on metabolic scaling for Q_{10} = 2 and Q_{10} = 3 from the largest extant turtles compared to actual maximum body size–temperature relationships for aquatic turtles (n= 270 species). (*B*) Model relationships for compared to actual for terrestrial turtles (*n* = 82 species). Black points represent coordinates for maximum carapace length and minimum MAT for the geographic ranges of extant species, and dark blue points represent coordinates for Shungura Formation specimens and isotopic MAT estimates (31). (*C*) LR model of the relationships between mean and maximum carapace lengths of aquatic turtle communities (*n* = 19,904 populated sampling points) sampled at 50-km spacing globally against local MAT. (*D*) LR for terrestrial turtles (*n* = 20,513 populated sampling points). Purple data points in *C* and *D* represent African communities, and dark blue data points represent Shungura Formation turtle coordinates as in *A* and *B*. Linear Regression best-fit lines are plotted in red for *C* and *D* with equations and R^2 values shown.

tropics, with fossil aquatic specimens comparable in size to the mean size of extant species, and terrestrial fossil sizes matching or exceeding the largest extant species globally but with higher MATs than predicted from Q_{10} curves. Several aquatic carapace lengths may be underestimates by up to 30% (*SI Appendix*, Table S1), but correcting for larger sizes does not substantially improve anomalies. MATs estimated from isotopic proxies may not necessarily represent the minimum MATs within the geographic ranges of Shungura Formation species; however, there is no evidence of extralimital distributions of eastern African turtles during the Plio-Pleistocene (e.g., refs. 35–38), and modern eastern African annual temperature variation is low. Applying the annual temperature range for modern Kenya to the presumed warmer Shungura temperature proxies would only lower estimates by, at most, 3.1 °C (33), to between 24 °C and 26 °C, which is well above modeled scaling curves.

The Predictive Power of Turtle Body Size as an Ecometric Is Stronger at Continental than at Global Scales. Although we found a positive association between global body size and temperature distributions for both aquatic and terrestrial turtles using LR (Fig. 2 *C* and *D*), the predictive power of these relationships is low. Using SDM projected ranges to build ecometric communities used in ML modeling significantly improved performance relative to communities based on raw occurrence points for multiple subsamples of the complete community dataset, including for global MAT predictions (*SI Appendix*). Regardless, no single community size statistic pairing stood out as having the strongest predictive relationship with temperature (Fig. 3). Overall, prediction anomalies were high at global and continental scales, as evidenced by SDs of the prediction anomalies across test points for LR and ML models (Table 1). The SD of the anomaly distribution, around 6 °C, is equal to that of the observed temperatures at all modern sampling points.

ML models trained on individual continents had significantly lower prediction anomalies than globally trained models, with an average MAT anomaly of 3.4 °C and an average MAP anomaly of 422 mm (Table 2). At the smaller spatial scale of the continent-specific analyses, linear relationships between turtle community body size statistics and temperature are stronger in some cases. For Asia, Europe, and Africa, the top five linear models were more likely to have significantly lower mean prediction anomalies than the top five ML models for those continents. ML models for Australia, North America, and South America had significantly lower anomalies in the majority of comparisons, as observed for the global models, suggesting that these continents' turtle faunas have weaker filtering of turtle size by climatic conditions than the other continents where linear models predict temperature more accurately. These contrasting patterns in model performance, along with low accuracy of globally trained models, do not support a strong universal relationship between these size statistics and temperature or precipitation.

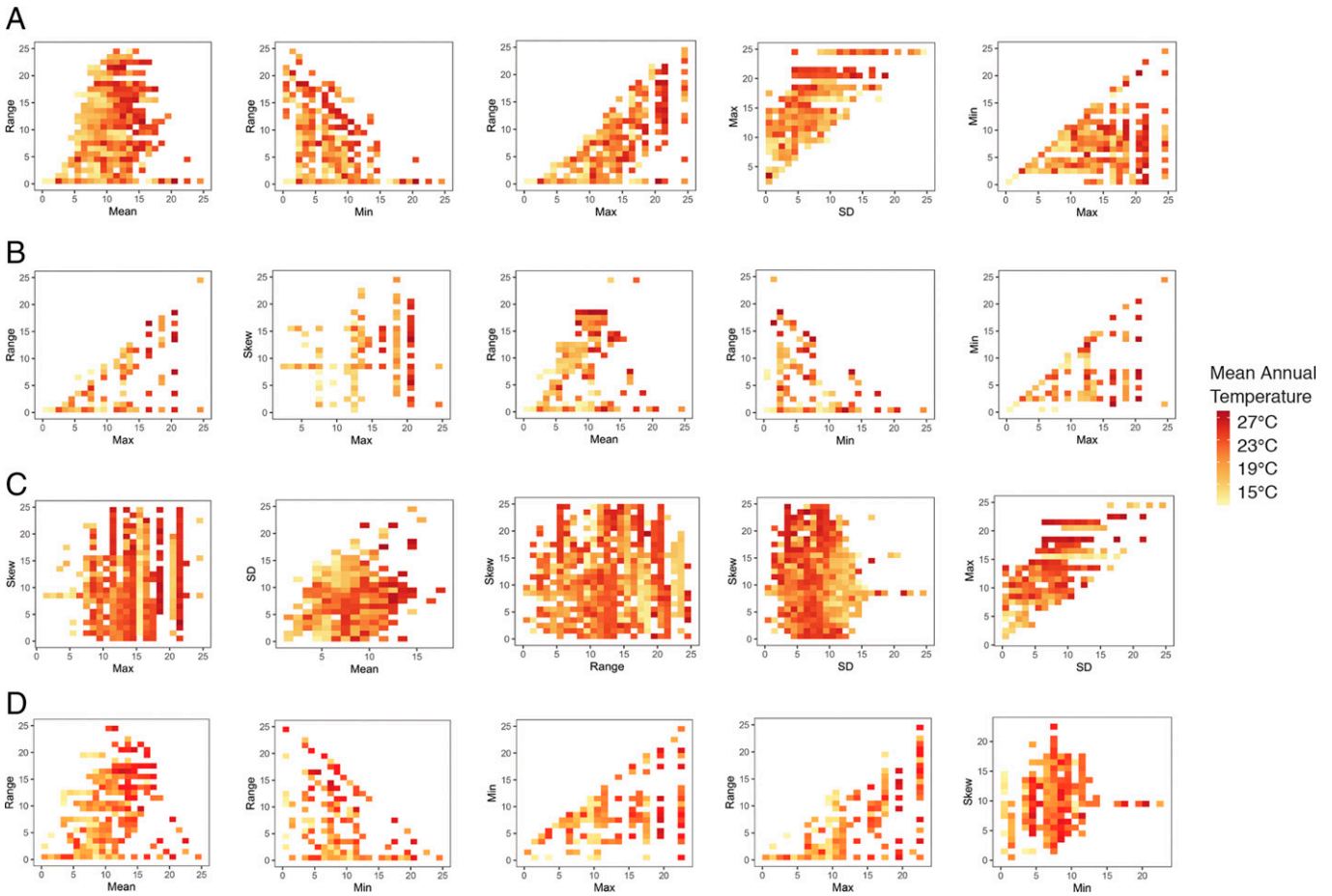

Fig. 3. MAT ecometric spaces of extant turtle communities for the top five ML models, trained for (*A*) all species globally, (*B*) global aquatic communities, (*C*) global terrestrial communities, and (*D*) all species within Africa. Each model is based on two statistics summarizing the distribution of turtle body sizes at community sampling points. The color of each cell represents the ML prediction for MAT from sampled communities falling into that combination of bins, with 25 bins defined for the range of each statistic's values across communities. These top-performing models had the lowest prediction anomalies for temperature at community test points. All models figured are trained in the SDM 5000_25 geographic dataset (*SI Appendix*).

Turtle Paleocommunity Ecometrics Coarsely Track Other Climate Proxy Estimates at Regional Scales. MAT estimates for the Shungura Formation from ML and LR ecometrics underestimate values relative to independent proxies (Fig. 4) (*SI Appendix*, Table S2). ML estimates range from 16.9 °C to 24.7 °C, and LR range from 21.0 °C to 24.0 °C compared to 27.0 °C 28.7 °C from pedogenic isotopes (31) (see *Materials and Methods*). ML MAP reconstructions range across members from 96.4 mm to 556.8 mm, and LR range from 1,032.4 mm to 1,155.1 mm, compared to ranges of 516 mm to 982 mm based on mammalian community structure (32) (Fig. 4). Although offset in absolute values, ecometric estimates generally track trends for other proxies for MAT estimates and MAP estimates, except for ML from members C through E. ML MAP estimates are erroneously low except for in member E, where they correspond with mammalian proxy estimates, and LR MAP estimates show a slight increase in precipitation from member C on, unlike mammalian proxy estimates, which show increasing aridity through the younger members of the Shungura Formation (32). Erroneously low ML MAT estimates for

Table 1. Comparisons between the five best and worst models from the global ecometric models, showing the number of pairwise comparisons where a model from one method had significantly lower prediction anomaly than a model from the other

Variable modeled		SDM vs. LR model anomaly comparison	SDM average mean anomaly	LR average mean anomaly	SDM average SD	LR average SD
Temperature (SDM 10x_25 vs. LR)	Best	25 vs. 0	−0.92 °C	1.2 °C	6.24 °C	5.53 °C
	Worst	15 vs. 10	0.95 °C	1.34 °C	5.9 °C	5.94 °C
Precipitation (SDM 5000_25 vs. LR)	Best	25 vs. 0	−73.9 mm	−245.3 mm	497.2 mm	720.2 mm
	Worst	25 vs. 0	−93.4 mm	−287.3 mm	567.2 mm	748.3 mm

The mean and SD of each model type's prediction anomalies are listed.

Table 2. Counts of pairwise comparisons for continental models between the best five ML models and one- and two-variable LR models for temperature and precipitation where the mean and distribution of prediction anomalies are significantly different, with the average SD in prediction anomalies for the compared models

Continent	ML vs. LR MAT	Average SD for best ML MAT (°C)	Average SD for best LR MAT (°C)	Range Maps vs. LR MAP	Average SD for best five ML MAP (mm)	Average SD for best five LR MAP (mm)
Africa	4 vs. 21	3.04	3.47	25 vs. 0	388.5	560.7
Asia	10 vs. 15	3.34	2.54	25 vs. 0	649.4	960.5
Australia	20 vs. 5	2.75	3.5	20 vs. 5	525.3	930.5
Europe	5 vs. 20	3.54	3.56	25 vs. 0	211.1	305.4
North America	25 vs. 0	5.6	7.9	25 vs. 0	569.4	832.3
South America	17 vs. 3	2.18	2.0	9 vs. 13	537.1	619.9

All ML models compared here trained in the Range Maps dataset (*SI Appendix*).

member F correspond to a decrease in terrestrial turtle carapace length. Large tortoises appear to be absent from the member despite comparatively large turtle sample sizes, which may represent transient ecological conditions independent of climate. Despite low accuracy in general application, global ML models estimate MATs for the Shungura Formation between 18.46 °C and 27.3 °C and more closely track changes in isotopic values than the Africa-specific models (*SI Appendix*, Table S2), likely due to the absence of giant terrestrial turtle body sizes in the African ecometric models (see below). Global ML MAP estimates range from 96.4 mm to 1,967.8 mm (*SI Appendix*, Table S2). Although MAP estimates for members D and G are erroneously high, their relative increases correspond to intervals identified as increasingly humid (39–41).

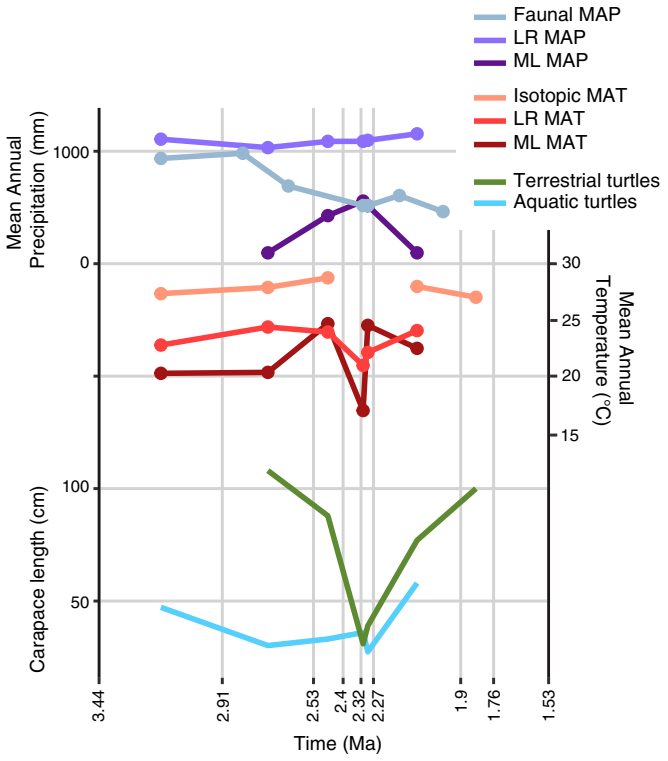

Fig. 4. Temperature and precipitation reconstructions for members B through H of the Shungura Formation from ecometric models compared to coeval local climate proxy estimates and maximum carapace lengths of Shungura Formation turtle communities. Faunal MAP values from ref. 32, and isotopic MAT values derived from ref. 33.

Discussion

The inverse relationship between maximum carapace lengths and MAT anomalies indicates that metabolic scaling with temperature may be an important functional factor for large body sizes, as has been proposed for size extremes in other poikilotherms (42, 43). However, large anomalies for smaller body sizes suggest metabolic scaling has limited influence on body size–temperature relationships for the majority of taxa, which may, instead, be sorted by functional factors related to biotic interactions and development (15, 16). This is additionally reflected in ecometric modeling, where maximum size as a community statistic did not perform better against temperature than other measures, including mean turtle size (Fig. 2) (23). The complexity of body size dynamics in extant turtles is also reflected in the Shungura fossil record, which does not track metabolic scaling for either aquatic or terrestrial taxa. Instead, the Shungura record is composed of taxa and communities whose body sizes and temperature relationships are a mixture of modern eastern African distributions and nonanalog sizes, suggesting that metabolism has not been a dominant functional factor for body size sorting in the past as well as the present.

Although lower than temperature estimates from isotopic proxies and modern temperatures of 27.8 °C for the Turkana Basin (33, 44), ecometric estimates are not inconsistent with habitat reconstructions for the Shungura Formation, which point to a more wooded and less arid environment than modern (45). Presuming isotopic MAT estimates exceed minimum MAT for the geographic ranges of eastern African taxa by several degrees, Africa-specific ecometric temperature estimates would be within 1 °C to 4 °C of isotopic estimates (Fig. 4), and global ML estimates would be equivalent. MAP in the modern Turkana Basin is 268 mm/y, whereas the ML ecometric models are similar to other proxies in estimating higher MAPs across the different members. Higher past precipitation is expected based on the mammal fossil record and carbon isotope values indicative of higher woody cover than is present today (30, 46, 47). Concordance in trends between proxies for several members additionally suggests these ecometrics can track regional climate change through time, just not with precision.

Offset between Africa-specific ecometrics and other proxy estimates may be due to changing functional factors driving body size distributions in Plio-Pleistocene communities, including differences in trophic structure and faunal composition (e.g., refs. 48–50). Alternatively, offset may be a modeling artifact due, in part, to nonclimatic factors in the origins of body size compositions of extant African turtle communities. Although community composition and size maxima of aquatic

turtles within the Shungura Formation do not demonstrate a significant difference from modern eastern African faunas (Fig. 2*C*), terrestrial turtles include size maxima greater than any extant taxon on the continent (Fig. 2*D*). The extinction of tortoises in excess of 1-m carapace length in the last million years in the Turkana Basin may have been driven, in part, by human exploitation, as tortoise butchery has been documented at Late Pleistocene archaeological sites (51, 52). Thus, the better fit of global ML MAT to isotopic proxy estimates may result from those models incorporating extant giant tortoise records that are absent from the Africa-specific models, due to human extirpation. Conversely, similarities in size structure between Shungura Formation aquatic turtle communities and modern eastern Africa faunas do not indicate human pressures as a functional factor for aquatic turtle body size distributions, despite evidence of predation by *Homo* species by the Early Pleistocene of eastern Africa (53).

The centrality of body size to many factors in ecology and life history (54), combined with relative ease of measurement, makes it a powerful tool for examining response to environmental change (15, 16, 55). However, the multivariate nature of the relationship of size to habit and habitat can also obfuscate a clear functional factor or single trait–environmental relationship such as those for anatomies specialized for constrained interactions like locomotion or feeding (e.g., refs. 56–58). As an ecometric, turtle body size does not have a single, powerful predictive functional relationship with environmental variables either globally or at continental scales. This lack of accuracy, combined with the absence of an identifiable functional factor to explain size distributions, hampers the ability to precisely estimate past environment based on this trait, suggesting that it will have a limited capacity for forecasting community climate responses unless used in conjunction with other traits.

It may be, as with our Africa-specific ecometrics, that human behaviors, including habitat modification and predation, have already degraded trait–environmental relationships in many cases to the point where the modern record can no longer provide accurate estimates of trait capacity in response to non-anthropogenic environments and environmental change. Our incorporation of SDMs into trait modeling is a useful approach for potentially minimizing the influence of human impacts on trait–environmental signals. For turtle body sizes, low predictive accuracy, despite cases of model improvement using SDM methodology, for ecometric models trained across all datasets suggests fundamental disruption to climatic signals by human and/or other biotic drivers. Ultimately, it may be that ecometric analyses of the fossil record, either by demonstrating trait consistency or changes in the presence or absence of human pressures (59), or in revealing trait occupancy breadth greatly in excess of that predictable from the modern world (e.g., refs. 42, 60, and 61), will be a more useful tool for forecasting the future.

Materials and Methods

Turtle Size and Climate Data. We collected size data for extant species as carapace length (centimeters), from literature sources (Dataset S1). Fossils were collected in the framework of the International Omo Research Expedition (IORE; 1967–1976) and of the Omo Group Research Expedition (OGRE; since 2006) with the authorization of the Authority for Research and Conservation of the Cultural Heritage. We measured carapace lengths for testudinid, trionychid, and pelomedusid turtles from members B through H of the Shungura Formation based on field research (OGRE) and collections (IORE + OGRE) in the National Museum of Ethiopia (NME)/Authority for Research and Conservation of the Cultural Heritage (ARCCH) to assemble ecometric paleocommunities (*SI Appendix*, Table S1). We drew climate data from WorldClim (44) (2.5-min resolution) to find both the minimum MAT for each extant turtle species (Fig. 2 *A* and *B*) and the MAT and MAP at each global community sampling point that we used for ecometric models. We calculated MATs for Shungura Formation members from an LR model based on published estimates of modern low-latitude soil temperatures and MAT (33) (*SI Appendix*).

Metabolic Scaling. We modeled the relationship between body size as carapace length and the minimum MAT available with species' geographic ranges to support effective metabolism using the model proportionality of body size differences to ambient temperature differences for poikilotherms for a given mass-specific metabolic rate (17), where the equation is solved for temperature of one taxon relative to its size and the size and temperature of a larger model taxon in order to estimate past size–temperature relationships based on fossil data (42, 43),

$$MAT_1 = MAT_2 + 3\alpha\ 10\ ^{\circ}\mathrm{C}\ \frac{\mathrm{Log}_{10}\left(\frac{L_1}{L_2}\right)}{\mathrm{Log}_{10}Q_{10}},$$

where MAT_1 is modeled minimum MAT from carapace length, MAT_2 is minimum MAT from the geographic range of the largest turtle taxon, α is the metabolic scaling exponent (whole body metabolic rate/surface area) of 0.25 for turtles based on metabolic rate equations (62), L_1 is modeled carapace length, and L_2 is carapace length of the largest turtle taxon. Q_{10} generally varies between two and three for metabolically efficient temperatures in reptiles (63, 64), and we use these values to model a range of temperature–size relationships.

We used the maximum size of *Chitra indica* with a carapace length of 150 cm at MAT of 20.2 °C to construct size–temperature scaling curves for aquatic taxa and the maximum size of *Chelonoidis nigra* with carapace length 130 cm at MAT of 22 °C to construct curves for terrestrial taxa (*SI Appendix*, Table S1). We calculated temperature anomalies as the difference between Q_{10}-modeled temperatures from carapace length in extant and fossil taxa and actual minimum MATs from modern distributions and MATs estimated from isotopic proxies in the Shungura Formation (Dataset S1).

Community Ecometric Modeling. We employed LR and ML methods to build ecometric models relating turtle community body size distributions to temperature and precipitation. Our linear models used single- and two-variable predictors from turtle community size mean, SD, maximum, minimum, range, and skewness (*SI Appendix*).

We adapted the ML approach from ref. 8, to output the most likely value for the environmental variable for a given trait distribution based on the observed environmental values across turtle communities in a training dataset. This method does not require a predictable relationship between the ecometric statistic values and the estimated climate variable. We extensively tested different techniques for building ML models, using 75% of the available community samples at global and continental scales to train the models and the remaining 25% of data points to test their predictive performance. (*SI Appendix*).

We compared models built using community sampling points drawn from three different geographic datasets. The first dataset is species range maps from the Turtle Taxonomy Working Group (65), and the second is species occurrence points from the Global Biodiversity Information Facility database (https://www.GBIF.org), both of which we used to assemble communities at a set of global sampling points spaced at 50 km across the terrestrial globe. The third input dataset we used is range maps derived from SDMs (66). SDMs have not previously been employed in ecometric modeling, but their estimates of geographic areas where environmental conditions are suitable for each species can improve ecometric community sampling, because the SDMs output an approximation of ranges prior to human impacts on geographic distributions.

We also compared ML models using only occurrences of terrestrial or aquatic turtle species to investigate whether body size is more strongly related to climate in turtle communities from one of these habitat categories. We built additional models based only on training points on each continent and compared their predictive performance for temperature and precipitation with that of global models at test points on individual continents (Table 1). We provide the full ranking of

models in each run and comparisons of prediction anomalies between datasets, along with all results for precipitation modeling (*SI Appendix*).

We applied ecometric models to reconstruct temperature and precipitation values for each member of the Shungura Formation based on paleocommunity ecometrics. We inputted these communities into the top-performing models to estimate temperature and precipitation at the member stratigraphic scale.

Data, Materials, and Software Availability. All specimen data are listed in supporting information. Modern turtle occurrence and range data are from sources cited in text. R code for ecometric analyses is in (8) and R code for SDMs is in (66).

ACKNOWLEDGMENTS. We thank the members of the Head Lab for discussion and support, as well as Michelle Lawing and Jenny McGuire for discussion and assistance in developing this project. Thanks go to Rachel Short and John Jacisin for assistance in developing ML ecometric methods, and to Ben Shipley for assistance with building SDMs and geographic analyses. For access to specimens, we thank the NME/ARCCH and all staff members (notably, Tomas Getachew Bedane), and the staff of the University Museum of Zoology, University of Cambridge. We thank the numerous participants in the IORE and OGRE fieldwork, as well as the Ethiopian Authorities for granting research permissions and support. This research was funded by a Herschel Smith Fellowship, Emmanuel College Panton Trust and Gerard Evans Fund grants, and a Cambridge University Worts Travelling Scholars grant to A.K.P.; the Ministry of Europe and Foreign Affairs (France), the National Center for Scientific Research (France), the Fyssen Foundation, and National Agency for Research Project ANR-16-CE27-0009-01 to OGRE missions in Ethiopia; and Natural Enivronment Research Council grant NE/W007576/1 and National Science Foundation award 2124836 to J.J.H., with additional support from the Integrated Climate Change Biology and Conservation Paleobiology in Africa programs of the International Union of Biological Sciences to J.J.H and J.M.

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