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Quaternary megafauna extinctions altered body size distribution in tortoises

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The late Quaternary is characterized by the extinction of many terrestrial megafauna, which included tortoises (Family: Testudinidae). However, limited information is available on how extinction shaped the phenotype of surviving taxa. Here, based on a global dataset of straight carapace length, we investigate the temporal variation, spatial distribution and evolution of tortoise body size over the past 23 million years, thereby capturing the effects of Quaternary extinctions in this clade. We found a significant change in body size distribution characterized by a reduction of both mean body size and maximum body size of extant tortoises relative to fossil taxa. This reduction of body size occurred earlier in mainland (Early Pleistocene 2.588–0.781 Ma) than in island tortoises (Late Pleistocene/Holocene 0.126–0 Ma). Despite contrasting body size patterns between fossil and extant taxa on a spatial scale, tortoise body size showed limited variation over time until this decline. Body size is a fundamental functional trait determining many aspects of species ecologies, with large tortoises playing key roles as ecosystem engineers. As such, the transition from larger sized to smaller sized classes indicated by our findings likely resulted in the homogenization of tortoises' ecological functions and diminished the role of tortoises in structuring the vegetation community.

1. Introduction

Large-bodied terrestrial herbivores, generally referred to as megafauna, became extinct in large numbers during the late Quaternary (50 000–10 000 years before present) [1,2]. Broad-scale megafauna extinctions shifted the body size distribution within surviving populations or communities toward a higher proportion of small-bodied animals [3]. Such changes can have severe consequences for ecosystem functioning because megafaunal species provide ecosystem services not easily compensated by smaller sized species [3–6]. For example, megaherbivores consume large amounts of specific plants and cycle nutrients, thereby shaping the environment they inhabit [7–10] and affecting plant population dynamics (including growth, densities and dispersal distances) [6,11]. Accordingly, studying size-biased extinction events and associated macroevolutionary shifts in body size might help explain ecological patterns present today [9,12].

Large-sized reptiles experienced high rates of extinctions during the late Quaternary but have been much less studied than mammals which are the focus of a majority of studies investigating the consequences of species extinctions on body size [1,2,5,6,12–17]. For instance, numerous species of giant (carapace lengths of ≥1.5 m; e.g. *Titanochelon schafferi*, *Megalochelys atlas* [14]) tortoises (Family: Testudinidae) were abundant during most of the Pleistocene until becoming extinct before the Holocene (22 species of the family Testudinidae, five species of the family Meiolaniidae) [7,14,17,18]. Extinction rates of tortoises proportionally increased on islands compared to the mainland as 80% of extinctions during the Holocene and 100% of extinctions since the year 1500 affected island-living tortoise species (16 species of the family Testudinidae and the last 2 species of the family Meiolaniidae) [14,17]. As such, large body size and insularity have been identified as playing important roles in the extinctions of tortoise taxa [17], with giant tortoises only persisting on two remote archipelagos today: the Galápagos islands and the Aldabra Atoll [14]. These giant tortoises are recognized ecosystem engineers and their loss has been found to cause declines in plant diversity and consequent habitat degradation [8–10]. The availability of fossil data provides the opportunity to describe the tempo and mode of body size variation in relation to extant tortoises [19].

Giant tortoises are common in the fossil record since the late Palaeogene [20–22] and causal explanations for their extinction during the Quaternary have been investigated [14]. The potential causes of extinction of large tortoises in the late Quaternary include hominin and human exploitation concomitant with global and local changes in climate and habitat [23,24]. These extinctions of terrestrial tortoises appear to be non-random, with the complete extirpation of species in the family Meiolaniidae and the highest proportion of extinctions among extant turtles in the family Testudinidae [14]. Intensive hunting and exploitation of specific tortoise populations by hominins have further been identified to cause a decrease in mean tortoise body size—sometimes so severe and with an obvious link to human activity that tortoise body size has been used to estimate human population density [25–27]. However, we still lack a comprehensive understanding of how body size distributions and dynamics in tortoises changed following extinctions on a global scale.

Body size is a key functional trait because it scales with many physiological and ecological processes, such as metabolic rate, locomotion, energetic demands, generation time, longevity, range size, predation, competition and even extinction risk [17,28–30]. Several studies have investigated body size patterns and distributions in extant turtles and tortoises [31–33], yet few have connected those observations to the fossil record [17,19]. The overall pattern in extant turtles and tortoises shows a right-skewed body size distribution such that small-bodied taxa are more abundant than large-bodied taxa [31–33]. Such a right-skewed body size distribution is common in the animal kingdom [34,35]. Although mainland tortoises and freshwater turtles exhibit a right-skew in the distribution of body size, insular tortoises display a left-skewed distribution, i.e. a higher frequency of large-bodied taxa [33]. Further, studies suggest that extant turtles and tortoises have habitat-dependent differences in body size optima, with freshwater turtles and mainland tortoises having a smaller body size optimum than marine turtles and island tortoises [31–34]. These differences in body size optima match investigations in the fossil record, which provide evidence of both gigantism and miniaturization in tortoises (family: Testudinidae) [19]. Although body size data of fossil and extinct turtles and tortoises is available and many studies investigate body size patterns in extant turtles and tortoises, much less is known about how extant body size patterns compare with patterns from the fossil record.

Here, we investigate the temporal pattern of variation in body size in fossil and extant tortoises (family: Testudinidae) over the last 23 million years, i.e. from the Early Miocene throughout the Quaternary until today. Specifically, we asked how the megafauna extinction affected body size patterns in tortoises. To answer our research question, we first compare body size distributions over time between island and mainland species. Second, we assess the differences in mean body size between fossil and extant tortoises in both the mainland and on islands. Lastly, we evaluate the tempo and mode of body size evolution over the entire time series. Our results show that the Quaternary megafauna extinction resulted in a clear shift in tortoise body size and we discuss possible implications for ecosystem function.

2. Material and methods

(a) Data collection

We obtained body size data for fossil and extant tortoises (Family: Testudinidae) from several sources. We used midline straight carapace length (SCL, in mm) as our measurement of body size. Midline SCL is the most common metric for body size in turtles in the literature and allows comparison with other published results even though it does not account for the dome shape of the turtle shell [14,31–33]. Fossil data were gathered from the late Early Miocene until the Holocene (23-0.0117 Ma). We used the FosFarBase (http://www.wahre-staerke.com, last accessed March 2017), the Paleobiology Database (PBDB; http://paleobiodb.org, last accessed July 2018), and Rhodin *et al.* [14] to identify key references (see electronic supplementary material, table S1). We obtained body size values for the fossil taxa from the primary literature and in some cases from the PBDB. The fossil data consists of 390 records and includes additional information on taxonomy, localities ($n = 196$) and age (electronic supplementary material, table S2, figure S1). Locality age was available at the stratigraphic stage level in most cases. We binned the age data to ensure a comparable sample size among bins (e.g. the two earliest stages of the Miocene were lumped in a single time bin; table 1). In the binned data 13 of 31 fossil genera were not sampled in one or more time bins between their first and last occurrences. Rather than assume the presence of the genera in those intervening time bins, we treated them as missing values instead of estimating body size (further details on the data treatment are provided in the SOM, electronic supplementary material, figure S4). For extant tortoise taxa, we collected SCL data by both measuring specimens from the collection of the Museum für Naturkunde Berlin ($n = 67$) and gathering body size data from the literature (electronic supplementary material, table S2, $n = 173$). In total, we collected data from 31 genera and 169 species across fossil and extant tortoises (electronic supplementary material, tables S1 and S2).

(b) Body size estimation

For some fossil specimens ($n = 99$) the carapace was not preserved or was too incomplete to measure SCL. In these cases, we used other skeletal elements such as plastron length (PL) and appendicular elements to estimate SCL (electronic supplementary material, table S1). For SCL estimation from PL, we used multivariate imputation by chained equations from the R package *mice* [36] to extrapolate missing data via a Bayesian linear regression (method = 'norm', electronic supplementary material, figure S2) from extant and fossil taxa. For SCL estimations from femora and humeri, we used ratios between the appendicular elements and SCL based on Hutterer *et al.* [37] and Franz *et al.* [38], respectively. Several publications provided scaled figures instead of measurements, from which we measured either SCL directly or PL, humeri or femora lengths for estimating SCL.

(c) Analyses

All analyses were performed in the R software environment [39,40]. First, we generated randomized sample-based accumulation curves using the *vegan* package [41] to determine if our sampling was sufficient to capture the diversity of tortoises over the past 23 Myr (discussion of preservation bias is in the SOM).

Table 1. Descriptive statistics of straight carapace length (SCL) for the entire dataset (all) as well as different subgroups, i.e. per time bin (min - max Ma), extant and fossil tortoises, mainland and insular taxa in general and for extant and fossil tortoises separately. The table contains sample sizes (on individual, species and genus levels), minimum, maximum, mean, median, variance, skewness, kurtosis, as well as the corresponding log values of straight carapace length. Apart from the most recent time bin, which includes all extant genera, the Early Pleistocene contains the highest sample size.

group	individuals	species	genera	min SCL	max SCL	CL	median SCL	variance	skewness	kurtosis	log mean SCL	log median SCL	log skewness	log kurtosis
all	630	169	31	80.0	2500	434.7	270.0	164 134.09	2.14	7.99	5.8	5.6	0.69	2.73
recent (0-0.0117 Ma)	252	64	18	80.0	1300	329.3	242.2	67 449.64	1.85	5.92	5.6	5.5	0.59	2.72
Late Pleistocene (0.0117-0.126 Ma)	50	19	8	102.4	1250	446.9	342.4	68 527.81	1.16	3.58	6.0	5.8	0.22	2.50
Middle Pleistocene (0.126-0.781 Ma)	53	13	7	132.0	1800	389.2	293.0	97 470.85	3.03	12.27	5.8	5.7	1.42	5.51
Early Pleistocene (0.781-1.806 Ma)	57	27	12	96.5	2000	463.1	263.8	161 825.86	1.75	5.77	5.9	5.6	0.71	2.43
Gelasian (1.806-2.588 Ma)	31	14	8	118.9	2050	553.5	194.9	407 449.36	1.31	3.14	5.8	5.3	0.93	2.11
Piacencian (2.588-3.6 Ma)	21	14	9	90.0	1600	606.1	428.0	274 229.86	0.99	2.49	6.0	6.1	0.02	2.03
Zanclean (3.6-5.332 Ma)	26	14	8	164.9	2500	952.0	857.5	478 925.31	1.10	3.56	6.6	6.8	−0.42	2.32
Messinian (5.332-7.246 Ma)	11	8	5	140.0	2100	919.7	729.6	552 706.72	0.38	1.64	6.4	6.6	−0.24	1.42
Tortonian (7.246–11.608 Ma)	48	23	10	105.0	1540	444.8	250.0	172 995.44	1.55	3.93	5.8	5.5	0.85	2.64
Serravallian (11.608-13.82 Ma)	31	11	6	111.0	1500	373.3	220.0	159 888.34	2.15	6.12	5.6	5.4	1.46	4.11
Langhian (13.82-15.97 Ma)	14	10	7	270.0	1600	745.6	700.0	235 193.56	0.29	1.52	6.4	6.4	0.04	1.16
Burdigalian/Aquitanian (15.97-23.03 Ma)	36	16	10	113.0	1100	372.1	273.3	69 970.94	1.44	4.05	5.7	5.6	0.53	2.37
fossil	378	116	24	90.0	2500	505.0	285.4	216 559.77	1.84	6.16	5.9	5.7	0.66	2.43
insular	147	56	19	80.0	2000	578.0	500.0	159 787.40	1.01	3.94	6.1	6.2	−0.28	2.06
mainland	483	129	29	81.0	2500	391.1	250.0	157 622.64	2.64	10.49	5.7	5.5	1.05	3.70
extant insular	96	32	12	80.0	1300	471.3	353.0	118 529.81	0.82	2.48	5.9	5.9	0.01	1.77
extant mainland	156	41	15	81.0	830	241.9	221.0	16 402.64	1.97	8.58	5.4	5.4	0.29	3.01
fossil insular	51	26	10	150.0	2000	778.9	750.0	178 351.30	1.11	4.06	6.5	6.6	−0.37	3.14
fossil mainland	327	98	24	90.0	2500	462.3	270.0	209 518.11	2.11	7.29	5.8	5.6	0.93	2.96

These curves were created both at the species and genus level. Given that genera are better sampled than species (electronic supplementary material, figure S3A-B), we performed all subsequent analyses at the genus level (further details on the data treatment in SOM, electronic supplementary material, figures S4–S6).

(d) Body size distribution analysis

To explore body size distributions and means, we calculated the moments (mean, median, variance, skewness, kurtosis; table 1), and determined the range (minimum, maximum values; table 1) of SCL (raw and log-transformed) using the R package *moments* [42]. We compared body size distributions of fossil versus extant tortoises on islands and the mainland by fitting a non-parametric kernel density function to each group and calculating the areas of overlap (=overlap indices) [43–45] using the R package *overlapping* [44,45]. We further evaluated differences in mean body size between these groups using an unpaired Wilcoxon rank sum test. To assess for body size differences among adjacent time bins we used the Kruskal–Wallis test and Dunn's test for multiple comparison [46]. We further compared the maximum values between the early (2.588–0.5 Ma) and the late Quaternary (0.5–0.1 Ma) by conducting an outlier analysis. Lastly, we investigated the relationship between body size, latitude, and age using a generalized additive model (GAM) [47] (statistical details are in the SOM).

(e) Temporal body size variation

To investigate the mode of body size evolution, we used the *paleoTS* package [48]. First, we calculated the mean SCL per genus within time bins and then summarized total mean SCL per time bin. Since mean values were used for this analysis, we also included additional data based on published studies on extant tortoise species that provided data on means and standard deviations ($n = 1728$, electronic supplementary material, table S3) and incorporated them into our genus SCL means that were then summarized per time bin. We tested for three common models of trait evolution: stasis, where the trait mean fluctuates around a constant mean (no significant change); generalized random walk (GRW), where the trait mean increases or decreases over time (directional change); and unbiased random walk (URW), where the trait mean changes over time but without moving the trait in a specific direction (non-directional change). The latter model assumes that trait changes do not accumulate so as to generate a trend toward a larger or smaller mean value. Model fits were based on maximum-likelihood estimation and model support is reported as the small-sample Akaike information criterion (AICc), with the lowest values indicating the best-supported model (table 2). Model fitting was performed first for the entire dataset and in separate analyses for mainland and island taxa.

3. Results

(a) Body size distributions

We found that tortoise body size exhibits a bimodal and right-skewed distribution, indicating a higher proportion of smaller rather than larger body sizes (table 1; figure 1*a*). The pattern of bimodality with two body size peaks is maintained when splitting the data into fossil and extant taxa, with an overlap of 70% between the two distributions (figure 1*b*). We also detected a bimodal body size distribution when comparing mainland and island taxa. By contrast to the pattern found between fossil and extant tortoises, the body size distribution of mainland taxa is right-skewed while island taxa are left-skewed, resulting in an overlap of 37% (figure 1*c*). When comparing the body size distributions of fossil and extant taxa across mainland and insular habitats, we found an overlap index of 45% and 66%, respectively (figure 1*d*). Further, we observed that on islands extant tortoises exhibit a platykurtic body size distribution whereas fossil taxa show a unimodal left-skewed distribution (figure 1*d*). On the mainland, extant tortoises exhibit a unimodal distribution whereas fossil taxa have binomial right-skewed distribution (table 1, figure 1*d*).

Table 2. Model-fitting results for the complete dataset as well as mainland and insular subsets comparing three models: generalized random walk (GRW), unbiased random walk (URW) and stasis. Stasis is the best-supported model (largest Akaike weights in bold) for all three datasets with the highest model support for insular data.

data	model	log likelihood	K	AICc	Akaike weight
all	stasis	−71.71	2	148.9	**0.851**
	URW	−75.36	1	153.2	0.103
	GRW	−74.63	2	154.8	0.046
island	stasis	−74.9	2	155.3	**0.708**
	URW	−77.72	1	157.9	0.195
	GRW	−76.89	2	159.3	0.097
mainland	stasis	−52.73	2	112.5	**0.941**
	URW	−123.9	1	250.5	0.000
	GRW	−55.51	2	118	0.059

(b) Body size trends over time and space

The mean body size of extant taxa is significantly smaller than fossil taxa in both insular and mainland habitats (islands: $W = 590.5$, $p < 0.01$; mainland: $W = 7095$, $p < 0.01$; figure 2*a*). This is also the case when comparing extant and fossil tortoises and insular and mainland habitats separately (extant versus fossil: $W = 23625$, $p < 0.01$, electronic supplementary material, figure S9A; insular versus mainland $W = 13963$, $p < 0.01$, electronic supplementary material, figure S9B). Pairwise comparisons of mean body size between adjacent time bins showed few significant differences (2/11 comparisons; figure 2*b*; electronic supplementary material, table S4): between the Late Pleistocene and the Recent ($p < 0.01$), and between the Langhian and Serravallian in the Middle Miocene ($p < 0.01$; figure 2*b*; electronic supplementary material, table S4). Finally, the smoothers from the GAM analysis for age and latitude were both significant. The GAM shows two peaks for both age and latitude. SCL shows a large peak around 7 Ma (Messinian) and a small peak around 14 Ma (Langhian) in age. Further, SCL shows a large peak around 0° (equator) and a smaller peak around 30° latitude (electronic supplementary material, figure S7). Body size declines toward the present and higher latitudes (electronic supplementary material, figure S7). Analysing outlier values only in the Quaternary identified maximum values for body size between 1800 and 2050 mm SCL in the early Quaternary (2.588–0.5 Ma) in contrast to outlier values between 1240 and 1300 mm SCL in the late Quaternary (see electronic supplementary material, figure S8).

(c) Evolutionary patterns

We found stasis to be the model that best described our data, with an Akaike weight of 85.1% (table 2). This was also the case for mainland and island tortoises, although model support was greater for the mainland than for the island taxa, 94.1%

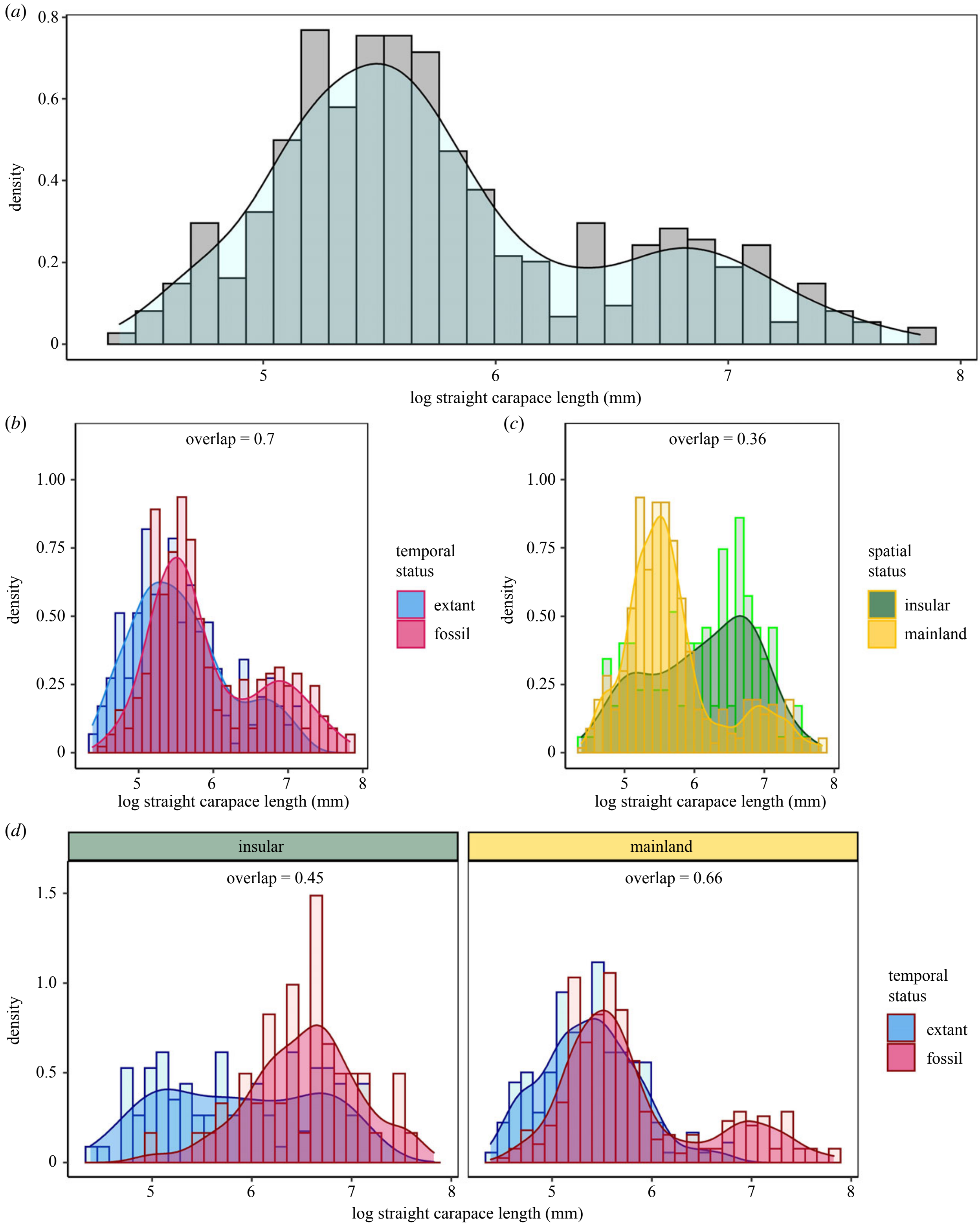

Figure 1. (*a*) Body size distribution of all tortoises is bimodal and right-skewed: small body sizes are the most frequent. (*b*) Temporal comparison of body size distribution shows extant and fossil taxa are both bimodal and right-skewed: small body sizes are more frequent than large body sizes. Body size overlap is high between fossil and extant tortoises. (*c*) Spatial comparison of body size distribution shows it is right-skewed and bimodal in mainland tortoises while it is left-skewed and bimodal in insular tortoises. Body size overlap is low between mainland and insular tortoises because of the contrasting skew. (*d*) Left: body size distribution of extant taxa on islands is rather uniform. Body size distribution of fossil taxa on islands is unimodal and, in contrast to all other groups, left-skewed: large body sizes are the most frequent. Body size overlap is low between fossil and extant tortoises in islands. Right: body size distribution of mainland tortoises is right-skewed for extant and fossil taxa and bimodal for fossil tortoises but unimodal for extant tortoises due to lack of large-bodied taxa. Body size overlap is high between fossil and extant tortoises on the mainland due to the preserved cluster of small-bodied taxa.

versus 70.8%, respectively (table 2). Body size trajectories are characterized by a gradual increase throughout the Miocene for tortoises overall and on the mainland (5.33–23 Ma; figure 3*a*). The increase in body size is consistent when analysing mainland taxa alone (figure 3*b*). On islands, the earliest record is from the Messinian (Late Miocene) and exceeded the body size of mainland species (figure 3*b*,*c*). For all tortoises, as well as on the mainland and on islands, body size reached a peak in the Messinian (Late Miocene) and Gelasian (Early Pleistocene). Following the first peak, body size declined during the Pliocene until another increase in the Gelasian. After this second peak, body size exhibited a striking decline,

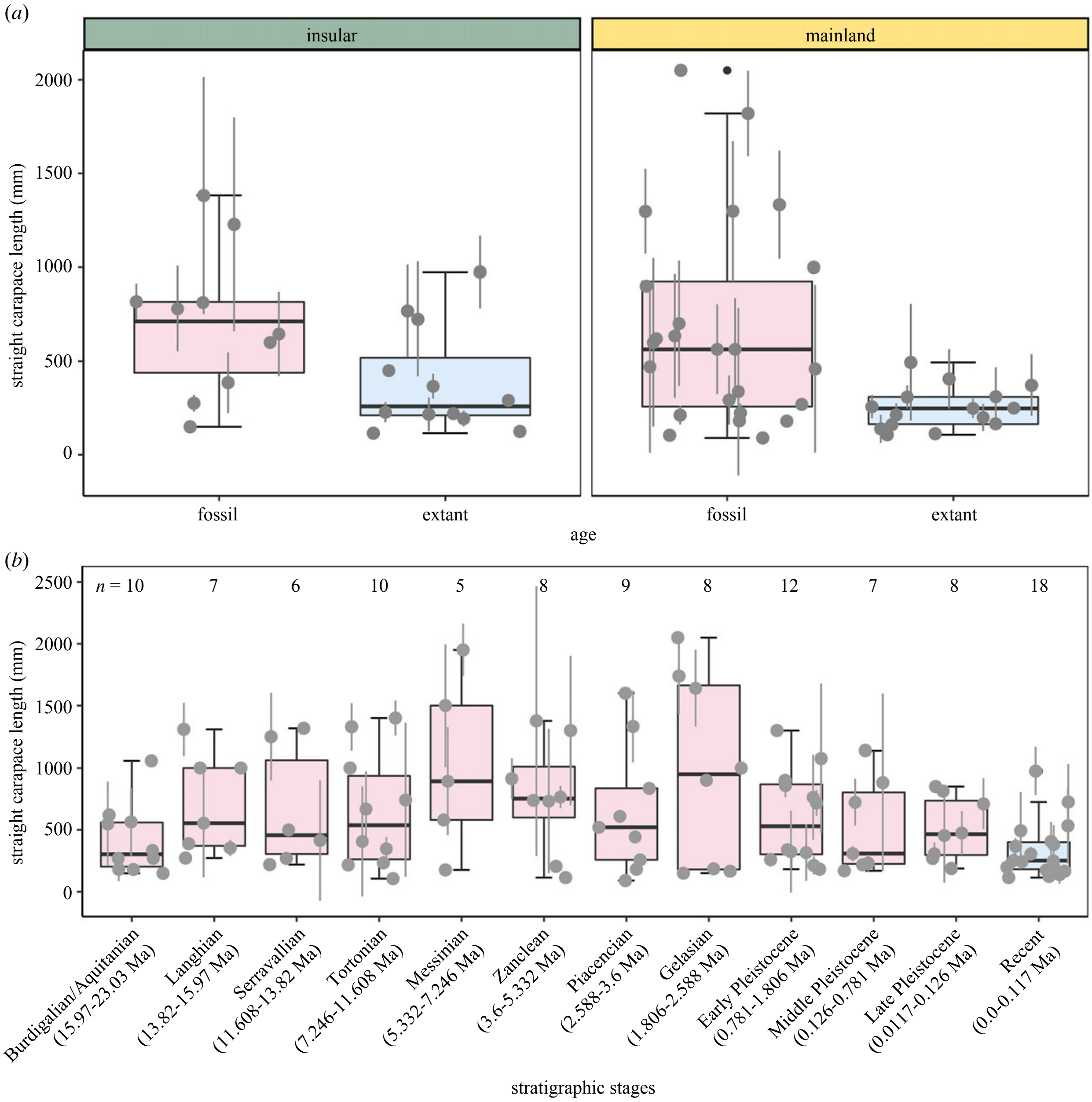

Figure 2. Comparison of tortoise body size on spatio-temporal scales. Bold lines indicate medians, boxes indicate lower and upper quartiles, whiskers indicate largest and smallest observations and outliers represent extreme values. Mean straight carapace length per genera are depicted as grey circles with error bars indicating the respective standard deviation. (*a*) Comparison of extant and fossil body size in island and mainland taxa. Extant tortoises have a smaller mean body size than fossil ones on both, islands and the mainland. (*b*) Comparison of straight carapace length across all time bins. Numbers refer to number of genera per group. Smallest average carapace length and variance is found in extant tortoises.

which was greater and occurred earlier in mainland compared to island taxa (figure 3*b*). Island taxa showed an initial gradual decline in body size from the Early Pleistocene to the Late Pleistocene followed by a second sharp decline at the Pleistocene–Holocene boundary (figure 3*c*).

4. Discussion

We found that the body size distribution of fossil and extant tortoises is bimodal and right-skewed (figure 1*a*). This pattern has been previously reported both in turtles and tortoises [19,31,33] and is common in the animal kingdom [34,35]. Our results further indicate that the late Quaternary extinctions resulted in a marked shift in body size distribution (figure 1, S8) and the reduction of mean body size from fossil to extant tortoises (figures 2 and 3). The change in body size distribution is more nuanced in island tortoises than in mainland taxa (figure 1*d*). In the mainland, there is a clear transition from a bimodal to a unimodal and skewed body size distribution. On islands, body size range is virtually the same between fossil and extant taxa, but the frequency of large-bodied taxa is lower in the extant sample, where the overall distribution is also more uniform (figure 1*d*). The contrasting body size distributions of fossil and extant taxa (figure 1*b*,*c*) is likely driven by the extinction of large-bodied species. This is corroborated by differences observed in average body size over time and space. Despite finding little variation of body size over time (figure 2*b*) and stasis as the general mode of body size evolution (figure 3*a*–*c*), extant tortoises are on average significantly smaller than their fossil conspecifics (even with extant giant tortoise genera *Aldabrachelys* on Aldabra and *Chelonoidis* on Galápagos reaching large body sizes greater than 1 m; figure 2*a*), a pattern also found in mammals [49], birds [5,13] and other reptiles [17,50].

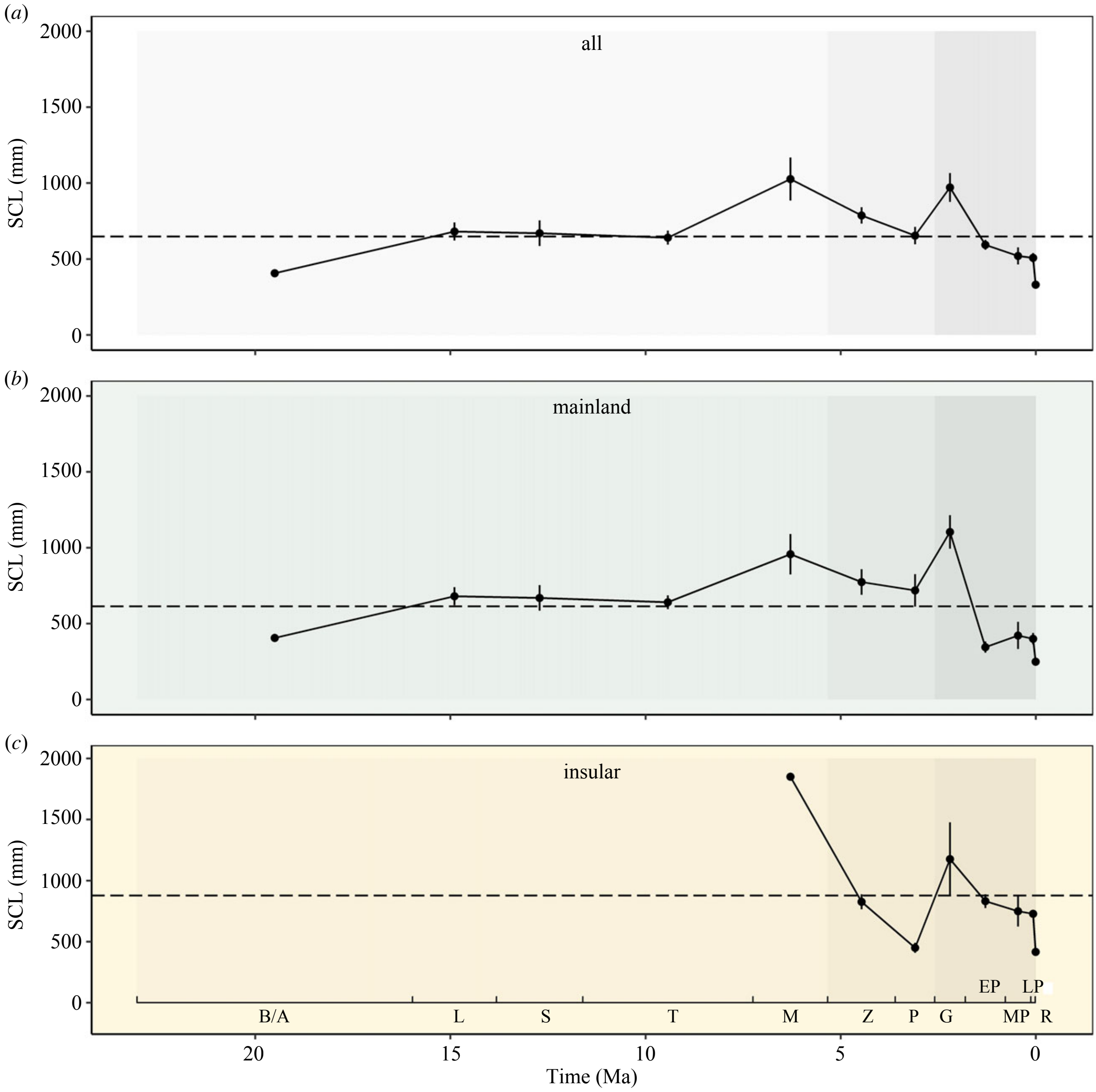

Figure 3. Evolutionary trajectory of straight carapace length (SCL) over time for (*a*) all taxa, (*b*) mainland taxa and (*c*) island taxa. Points and bars represent the mean carapace length within each time bin and standard errors, respectively. Black dashed line depicts the mean carapace length averaged across all time bins. Grey background indicates the different epochs: from the Miocene over the Pliocene to the Pleistocene (from light to dark). Letters indicate the stratigraphic stages from the Miocene to the Recent (B/A = Burdigalian/Aquitanian, L = Langhian, S = Serravallian, T = Tortonian, M = Messinian, Z = Zanclean, *p* = Piacencian, G = Gelasian, EP = Early Pleistocene, MP = Middle Pleistocene, LP = Late Pleistocene, R = Recent). Body size increases consistently until the Late Miocene (Messinian), briefly dips and rises again in the Pliocene and then steadily drops with onset of the Pleistocene for all tortoises and mainland tortoises. The oldest and largest island tortoises are known from the Late Miocene and also experience a dip and subsequent rise during the Pliocene and then drop during the Pleistocene.

We found significant differences in mean body size in two time intervals (Langhian–Serravallian, 15.97–11.608 Ma; Late Pleistocene–Recent, 0.0126–0 Ma; figure 2*b*). Interestingly, these shifts in mean body size coincide with different events in the earth's history: the transition from the Mid Miocene climatic optimum to the cooling trend of the younger Neogene and Quaternary [51,52], and the exploitation and extirpation of many tortoise species during the late Quaternary when humans and other hominins spread throughout the world. On a more local level, shifts in body size could be due to ecological stress caused by orogenic changes that altered the climate and prevailing habitat structure. For example, Cadena & Jaramillo [53] hypothesized that shifting geographical features such as the uplifting of the Andes and associated changes in river systems and drainages affected the distribution of Miocene turtles in South America. However, such local changes in body size are more difficult to investigate than large-scale patterns due to the incompleteness and bias of the fossil record (further discussion of impact on our results are in the SOM). Our observed shifts in body size occurred over short time intervals, and therefore they are not deemed significant when testing for the general mode of phenotypic evolution over the past 23 Ma, and accordingly the analysis supports stasis as the best fitting model to our data [54]. We suggest that the simultaneous trends of miniaturization and gigantism [19] yield a result of no shift in the mean body size of tortoises over time and as a consequence supports the pattern of stasis at the family level (electronic supplementary material, figure S10). Moreover, the distribution of genera throughout the time bins in our data as well as the heterogeneous dynamics of body size within genera, results in a uniform pattern of mean body size throughout the sampling period (electronic supplementary material, figure S11). In summary, mean body size of tortoises has not exhibited marked fluctuations over 23 Ma, but large and rapid changes have resulted in a smaller mean body size and shifted body size distribution patterns in extant tortoises relative to their fossil counterparts.

Phylogenetic analysis has provided refined insights into body size evolution across vertebrates [55–60]. However, we excluded phylogenetic comparative methods from our approach for two reasons. First, body size is an easily preserved trait for tortoises because of their hard bony shell. However, traits needed to infer taxonomy and subsequently estimate a phylogeny are scarcer in the fossil record of tortoises. For example, most phylogenies are based on skulls which, along with other appendicular elements, are often not preserved [61,62]. Second, the taxonomy of fossil tortoises is inconsistent, in part because fossil taxa have a history of being grouped and named based on body size alone [63]. Although the taxonomy of fossil tortoises has been revised in great detail in some regions and illuminated phylogenetic relationships of fossil taxa [18,61,62,64–69], there are still many fossil records that have not undergone recent taxonomic reevaluation. Such additional study is necessary to place the specimens into a broader phylogenetic context with confidence (for discussion of this issue see [18]). For these reasons, not conducting a phylogenetic analysis allowed us to include body size data from records lacking phylogenetic information as well as avoid a potential tautology due to the historical practice of naming fossil tortoise taxa based on size class, in conjunction with the heterogeneity of recent reexamination of this tradition (for a phylogenetic-focused approach to tortoise body size evolution see [19]).

Taken together, our results suggest a reduction of tortoise body size [49] as evidenced by an increase in the frequency of small taxa and the loss of bimodality in size distribution, and hence the large size peak (figure 1*a–d*). This was probably due to the extinction of the largest species during the late Quaternary [49]. The pattern of body size reduction occurred through different processes in mainland and island species. For example, mainland taxa went from two body size peaks to a single size peak, and island taxa moved from a left-skewed distribution to a uniform distribution in body size. The difference in timing of extinctions between mainland and islands has been attributed to the delayed arrival of humans on islands matching with the geographical extirpation patterns of tortoises [14], whereas discrepancies in body size patterns between mainland and island ecosystems might be due to specific habitats and associated changes [61,70]. Body size transitions such as those found here for tortoises have also been observed in terrestrial mammals following the late Quaternary extinctions [49,71]. However, general trends in the distribution of body sizes of insular mammals differ from those of insular tortoises [72], with insular mammals having mostly multimodal and right-skewed distributions [72]. The prevailing explanation for this pattern is that (herbivore) mammals generally adhere to the island size rule where small animals evolve larger body size on islands and vice versa [73]. Body size patterns of extant tortoises (i.e. larger species on islands than on the mainland) also seem to follow the island rule. However, biogeographic studies on dispersal patterns of tortoises and consideration of the fossil record have revealed that large-bodied taxa evolved on the mainland and later dispersed to islands where they became even larger, therefore contradicting the island rule [32,74]. The later extinction of all large-bodied tortoises on the mainland and almost all large-bodied tortoises in islands generated the body size pattern present in extant taxa [14].

The overall reduction in body size of extant turtles resulted in the homogenization of ecological functions, with potential severe consequences for ecosystem structure and function [9]. Multiple studies have shown a major role for larger bodied animals providing critical ecosystem services [3,4,13]. For example, giant tortoises are recognized to maintain ecosystems through grazing, browsing, trampling, selective feeding, nutrient cycling and seed dispersal [7,9,10]. Observational data suggest that smaller-sized animals can also be effective seed dispersers [75–79] and large size does not necessarily result in longer gut retention time [80]. However, megaherbivores play a more important role in this regard compared to smaller animals because they usually consume larger amounts of food and thereby seeds, can eat larger fruits, exploit a larger area and move over longer distances [3–6]. For example, the loss of mammalian megaherbivores has been associated with changes in plant communities, vegetation structure, biome shifts, fire activity and nutrient cycling [3,4,6]. Similarly, the disappearance of endemic, large tortoises on the Galápagos islands has resulted in the loss of wetland habitats [9]. The impact of the recent extinction of giant tortoises is so severe that rewilding programs with non-native extant giant tortoises have been developed to restore these lost ecosystem services [9,10]. While we can estimate the effect of giant tortoise extinctions on island ecosystems with some precision given that some taxa still remain and several extinctions are rather recent, the ecological impacts of giant tortoise extinctions on continents are less clear. Mainland tortoises were disproportionately affected by the extinction of megafaunal taxa with the eradication of all giant taxa on continents [14]. Mainland giant tortoises were not the largest herbivores in their respective communities and their ecological functions were shared with mammalian megafauna [13] in contrast to insular taxa, making giant tortoises on islands potentially less redundant and therefore more unique ecosystem engineers than on the mainland. Regardless of whether or not giant tortoises played unique ecological roles on the mainland, the sheer extent of their extinction in conjunction with mammalian megafauna extinctions likely altered ecosystem functioning [3,13].

In conclusion, based on the role of extant and recently extinct giant tortoises as ecosystem engineers, the body size reduction following the extinction of giant tortoises likely resulted in the homogenization of ecological functions and a large-scale reorganization of their ecosystems, especially on the mainland where none of the megafaunal species remain. Further research is needed to discern interactions of fossil giant tortoises with other extinct megaherbivores and their concrete niches and synergy within mainland ecosystems. Such investigations may provide more insight into community structures and impacts of community-wide megafauna loss.

Data accessibility. The datasets supporting this article have been uploaded as part of the supplementary material [81].

Authors' contributions. J.J.: data curation, formal analysis, investigation, methodology, project administration, software, validation, visualization, writing—original draft; C.P.: formal analysis, methodology, supervision, writing—review and editing; D.B.M.: conceptualization, formal analysis, methodology, supervision, visualization, writing—review and editing; J.M.: conceptualization, methodology, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interest.

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