

1 **Quaternary megafauna extinctions altered body size distribution in tortoises**

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11

12 **Abstract**

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

28 Keywords: late Quaternary extinction, size-biased extinction, body size downgrading,  
29 Testudinidae, carapace length, trait variation

30

## 31 **Introduction**

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

43 Large-sized reptiles experienced high rates of extinctions during the late Quaternary but have  
44 been much less studied than mammals which are the focus of a majority of studies investigating  
45 the consequences of species extinctions on body size [1,2,5,6,12–17]. For instance, numerous  
46 species of giant (carapace lengths of  $\geq 1.5$  m, e.g., *Titanochelon schafferi*, *Megalocheilus atlas*  
47 [14]) tortoises (Family: Testudinidae) were abundant during most of the Pleistocene until  
48 becoming extinct before the Holocene (22 species of the family Testudinidae, five species of the  
49 family Meiolaniidae) [7,14,17,18]. Extinction rates of tortoises proportionally increased on islands  
50 compared to the mainland as 80% of extinctions during the Holocene and 100% of extinctions  
51 since the year 1500 affected island living tortoise species (16 species of the family Testudinidae  
52 and the last 2 species of the family Meiolaniidae) [14,17]. As such, large body size and insularity  
53 have been identified as playing important roles in the extinctions of tortoise taxa [17], with giant  
54 tortoises only persisting on two remote archipelagos today: the Galápagos islands and the  
55 Aldabra Atoll [14]. These giant tortoises are recognized ecosystem engineers and their loss has

56 been found to cause declines in plant diversity and consequent habitat degradation [8–10]. The  
57 availability of fossil data provides the opportunity to describe the tempo and mode of body size  
58 variation in relation to extant tortoises [19].

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

71 Body size is a key functional trait, because it scales with many physiological and ecological  
72 processes, e.g., metabolic rate, locomotion, energetic demands generation time, longevity,  
73 range size, predation, competition and even extinction risk [17,28–30]. Several studies have  
74 investigated body size patterns and distributions in extant turtles and tortoises [31–33], yet few  
75 have connected those observations to the fossil record [17,19]. The overall pattern in extant  
76 turtles and tortoises shows a right-skewed body size distribution such that small-bodied taxa are  
77 more abundant than large-bodied taxa [31–33]. Such a right-skewed body size distribution is  
78 common in the animal kingdom [34,35]. Although mainland tortoises and freshwater turtles  
79 exhibit a right-skew in the distribution of body size, insular tortoises display a left-skewed  
80 distribution, i.e., a higher frequency of large-bodied taxa [33]. Further, studies suggest that

81 extant turtles and tortoises have habitat-dependent differences in body size optima, with  
82 freshwater turtles and mainland tortoises having a smaller body size optimum than marine turtles  
83 and island tortoises [31–34]. These differences in body size optima match investigations in the  
84 fossil record, which provides evidence of both gigantism and miniaturization in tortoises (family:  
85 Testudinidae) [19]. Although body size data of fossil and extinct turtles and tortoises is available  
86 and many studies investigate body size patterns in extant turtles and tortoises, much less is  
87 known about how extant body size patterns compare with patterns from the fossil record.

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

97

## 98 **Material & Methods**

### 99 *Data collection*

100 We obtained body size data for fossil and extant tortoises (Family: Testudinidae) from several  
101 sources. We used midline straight carapace length (SCL, in mm) as our measurement of body  
102 size. Midline SCL is the most common metric for body size in turtles in the literature and allows  
103 comparison with other published results even though it does not account for the dome shape of  
104 the turtle shell [14,31–33]. Fossil data were gathered from the late Early Miocene until the  
105 Holocene (23 – 0.0117 Ma). We used the FosFarBase (<http://www.wahre-staerke.com>, last  
106 accessed March 2017), the Paleobiology Database (PBDB; <http://paleobiodb.org>, last accessed  
107 July 2018), and Rhodin et al. [14] to identify key references (see Table S1). We obtained body  
108 size values for the fossil taxa from the primary literature and in some cases from the PBDB. The  
109 fossil data consists of 390 records and includes additional information on taxonomy, localities (n  
110 = 196) and age (Table S2, Fig. S1). Locality age was available at the stratigraphic stage level in  
111 most cases. We binned the age data to ensure a comparable sample size among bins (e.g., the  
112 two earliest stages of the Miocene were lumped in a single time bin; Table 1). In the binned data  
113 13 of 31 fossil genera were not sampled in one or more time bins between their first and last  
114 occurrences. Rather than assume the presence of the genera in those intervening time bins, we  
115 treated them as missing values instead of estimating body size (further details on the data  
116 treatment are provided in the SOM, Fig. S4). For extant tortoise taxa, we collected SCL data by  
117 both measuring specimens from the collection of the Museum für Naturkunde Berlin (n = 67) and  
118 gathering body size data from the literature (Table S2, n = 173). In total, we collected data from  
119 31 genera and 169 species across fossil and extant tortoises (Tables S1 and S2).

### 120 *Body size estimation*

121 For some fossil specimens (n = 99) the carapace was not preserved or was too incomplete to  
122 measure SCL. In these cases, we used other skeletal elements such as plastron length (PL) and

123 appendicular elements to estimate SCL (Table S1). For SCL estimation from PL, we used  
124 multivariate imputation by chained equations from the R package *mice* [36] to extrapolate  
125 missing data via a Bayesian linear regression (method = “norm”, Fig. S2) from extant and fossil  
126 taxa. For SCL estimations from femora and humeri, we used ratios between the appendicular  
127 elements and SCL based on Hutterer et al. [37] and Franz et al. [38], respectively. Several  
128 publications provided scaled figures instead of measurements, from which we measured either  
129 SCL directly or PL, humeri, or femora lengths for estimating SCL.

### 130 *Analyses*

131 All analyses were performed in the R software environment [39,40]. First, we generated  
132 randomized sample-based accumulation curves using the *vegan* package [41] to determine if  
133 our sampling was sufficient to capture the diversity of tortoises over the past 23 Ma (discussion  
134 of preservation bias is in the SOM). These curves were created both at the species and genus  
135 level. Given that genera are better sampled than species (Fig. S3A-B), we performed all  
136 subsequent analyses at the genus level (further details on the data treatment in SOM, Fig. S5 +  
137 S6).

### 138 *Body size distribution analysis*

139 To explore body size distributions and means, we calculated the moments (mean, median,  
140 variance, skewness, kurtosis; Table 1), and determined the range (minimum, maximum values;  
141 Table 1) of SCL (raw and log-transformed) using the *moments* R package [42]. We compared  
142 body size distributions of fossil vs. extant tortoises on islands and the mainland by fitting a non-  
143 parametric kernel density function to each group and calculating the areas of overlap (= overlap  
144 indices) [43–45] using the R package *overlapping* [44,45]. We further evaluated differences in  
145 mean body size between these groups using an unpaired Wilcoxon rank sum test. To assess for  
146 body size differences among adjacent time bins we used the Kruskal-Wallis test and Dunn’s test  
147 for multiple comparison [46]. We further compared the maximum values between the early

148 (2.588 – 0.5 Ma) and the late Quaternary (0.5 – 0.1 Ma) by conducting an outlier analysis.  
149 Lastly, we investigated the relationship between body size, latitude, and age using a generalized  
150 additive model (GAM) [47] (statistical details are in the SOM).

#### 151 *Temporal body size variation*

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



167 **Results**

168 *Body size distributions*

169 We found that tortoise body size exhibits a bimodal and right-skewed distribution, indicating a  
170 higher proportion of smaller body sizes than larger body sizes (Table 1; Fig. 1A). The pattern of  
171 bimodality with two body size peaks is maintained when splitting the data into fossil and extant  
172 taxa, with an overlap of 70% between the two distributions (Fig. 1B). We also detected a bimodal  
173 body size distribution when comparing mainland and island taxa. In contrast to the pattern found  
174 between fossil and extant tortoises, the body size distribution of mainland taxa is right-skewed  
175 while island taxa are left-skewed, resulting in an overlap of 37% (Fig. 1C). When comparing the  
176 body size distributions of fossil and extant taxa across mainland and insular habitats, we found  
177 an overlap index of 45% and 66% respectively (Fig. 1D). Further, we observed that on islands  
178 extant tortoises exhibit a platykurtic body size distribution whereas fossil taxa show a unimodal  
179 left-skewed distribution (Fig. 1D). On the mainland, extant tortoises exhibit a unimodal  
180 distribution whereas fossil taxa have binomial right-skewed distribution (Table 1, Fig. 1D).

181 *Body size trends over time and space*

182 The mean body size of extant taxa is significantly smaller than fossil taxa in both insular and  
183 mainland habitats (islands:  $W = 590.5$ ,  $p < 0.01$ ; mainland:  $W = 7095$ ,  $p < 0.01$ ; Fig. 2A). This is  
184 also the case when comparing extant and fossil tortoises and insular and mainland habitats  
185 separately (extant vs. fossil:  $W = 23625$ ,  $p < 0.01$ , Fig. S9A; insular vs. mainland  $W = 13963$ ,  $p <$   
186  $0.01$ , Fig. S9B). Pairwise comparisons of mean body size between adjacent time bins showed  
187 few significant differences (2/11 comparisons; Fig. 2B, Table S4): between the Late Pleistocene  
188 and the Recent ( $P < 0.01$ ) and between the Langhian and Serravallian in the Middle Miocene ( $P$   
189  $< 0.01$ ; Fig. 2B, Table S4). Finally, the smoothers from the GAM analysis for age and latitude  
190 were both significant. The GAM shows two peaks for both age and latitude. SCL shows a large  
191 peak around 7 Ma (Messinian) and a small peak around 14 Ma (Langhian) in age. Further, SCL

192 shows a large peak around 0 degrees (equator) and a smaller peak around 30 degrees latitude  
193 (Fig. S7). Body size declines towards the present and higher latitudes (Fig. S7). Analyzing outlier  
194 values only in the Quaternary identified maximum values for body size between 1800 and 2050  
195 mm SCL in the early Quaternary (2.588 – 0.5 Ma) in contrast to outlier values between 1240 and  
196 1300 mm SCL in the late Quaternary (see Fig. S8).

### 197 *Evolutionary patterns*

198 We found stasis to be the model that best described our data, with an Akaike weight of 85.1%  
199 (Table 2). This was also the case for mainland and island tortoises, although model support was  
200 greater for the mainland than for the island taxa, 94.1% vs. 70.8%, respectively (Table 2). Body  
201 size trajectories are characterized by a gradual increase throughout the Miocene for tortoises  
202 overall and on the mainland (5.33 - 23 Ma; Fig. 3A). The increase in body size is consistent  
203 when analyzing mainland taxa alone (Fig. 3B). On islands, the earliest record is from the  
204 Messinian (Late Miocene) and exceeded the body size of mainland species (Fig. 3B-C). For all  
205 tortoises, as well as on the mainland and on islands, body size reached a peak in the Messinian  
206 (Late Miocene) and Gelasian (Early Pleistocene). Following the first peak, body size declined  
207 during the Pliocene until another increase in the Gelasian. After this second peak, body size  
208 exhibited a striking decline, which was greater and occurred earlier in mainland compared to  
209 island taxa (Fig. 3B). Island taxa showed a first gradual decline in body size from the Early  
210 Pleistocene to the Late Pleistocene followed by a second sharp decline at the Pleistocene-  
211 Holocene boundary (Fig. 3C).

## 212 Discussion

213 We found that the body size distribution of fossil and extant tortoises is bimodal and right  
214 skewed (Fig 1A). This pattern has been previously reported both in turtles and tortoises  
215 [19,31,33] and is common in the animal kingdom [34,35]. Our results further indicate that the late  
216 Quaternary extinctions resulted in a marked shift in body size distribution (Fig. 1, S8) and the  
217 reduction of mean body size from fossil to extant tortoises (Figs. 2-3). The change in body size  
218 distribution is more nuanced in island tortoises than in mainland taxa (Fig. 1D). In the mainland,  
219 there is a clear transition from a bimodal to a unimodal and skewed body size distribution. On  
220 islands, body size range is virtually the same between fossil and extant taxa, but the frequency  
221 of large-bodied taxa is lower in the extant sample, where the overall distribution is also more  
222 uniform (Fig. 1D). The contrasting body size distributions of fossil and extant taxa (Fig. 1B-C) is  
223 likely driven by the extinction of large-bodied species. This is corroborated by differences  
224 observed in average body size over time and space. Despite finding little variation of body size  
225 over time (Fig. 2B) and stasis as the general mode of body size evolution (Fig. 3A-C), extant  
226 tortoises are on average significantly smaller than their fossil conspecifics (even with extant giant  
227 tortoise genera *Aldabrachelys* on Aldabra and *Chelonoidis* on Galápagos reaching large body  
228 sizes > 1 m Fig. 2A), a pattern also found in mammals [49], birds [5,13], and other reptiles  
229 [17,50].

230 We found significant differences in mean body size in two time intervals (Langhian –  
231 Serravallian, 15.97 – 11.608 Ma; Late Pleistocene – Recent, 0.0126 - 0 Ma; Fig 2B).  
232 Interestingly, these shifts in mean body size coincide with different events in the earth's history:  
233 the transition from the Mid Miocene climatic optimum to the cooling trend of the younger  
234 Neogene [51,52] and Quaternary and the exploitation and extirpation of many tortoise species  
235 during the late Quaternary when humans and other hominins spread throughout the world. On a  
236 more local level, shifts in body size could be due to ecological stress caused by orogenic

237 changes that altered the climate and prevailing habitat structure. For example, Cadena and  
238 Jaramillo [53] hypothesized that shifting geographic features such as the uplifting of the Andes  
239 and associated changes in river systems and drainages affected the distribution of Miocene  
240 turtles in South America. However, such local changes in body size are more difficult to  
241 investigate than large-scale patterns due to the incompleteness and bias of the fossil record  
242 (further discussion of impact on our results are in the SOM). Our observed shifts in body size  
243 occurred over short time intervals, and therefore they are not deemed significant when testing  
244 for the general mode of phenotypic evolution over the past 23 Ma, and therefore the analysis  
245 supports stasis as the best fitting model to our data [54]. We suggest that the simultaneous  
246 trends of miniaturization and gigantism [19] yields a result of no shift in the mean body size of  
247 tortoises over time and as a consequence supports the pattern of stasis at the family level (Fig.  
248 S10). Moreover, the distribution of genera throughout the time bins in our data as well as the  
249 heterogeneous dynamics of body size within genera, results in a uniform pattern of mean body  
250 size throughout the sampling period (Fig. S11). In summary, mean body size of tortoises has not  
251 exhibited marked fluctuations over 23 Ma, but large and rapid changes have resulted in a  
252 smaller mean body size and shifted body size distribution patterns in extant tortoises relative to  
253 their fossil counterparts.

254 Phylogenetic analysis have provided refined insights into body size evolution across vertebrates  
255 [55–60]. However, we excluded phylogenetic comparative methods from our approach for two  
256 reasons. First, body size is an easily preserved trait for tortoises because of their hard bony  
257 shell, but traits needed to infer taxonomy and subsequently build a phylogeny are scarcer in the  
258 fossil record of tortoises because they are based on skulls which, along with other appendicular  
259 elements, are often not preserved [61,62]. Second, the taxonomy of fossil tortoises is  
260 inconsistent, in part because fossil taxa have historically often been grouped and named based  
261 on body size alone [63]. Although the taxonomy of fossil tortoises has been revised in great  
262 detail in some regions and illuminated phylogenetic relationships of fossil taxa [18,61,62,64–69],

263 there are still many fossil records that have not been reevaluated taxonomically, which is  
264 necessary to put them into a larger phylogenetic context with confidence (for discussion of this  
265 issue see [18]). For these reasons, not conducting a phylogenetic analysis allowed us to include  
266 body size data from records lacking phylogenetic information as well as avoid a potential bias  
267 due to the historical practice of naming fossil tortoise taxa based on size class, in conjunction  
268 with the heterogeneity of recent reexamination of this tradition (for a phylogenetic-focused  
269 approach to tortoise body size evolution see [19]).

270 Taken together, our results suggest a reduction of tortoise body size [49], as evidenced by an  
271 increase in the frequency of small taxa and the loss of bimodality in size distribution and hence,  
272 of the large size peak (Fig. 1A-D). This was likely due to the extinction of the largest species  
273 during the late Quaternary [49]. The pattern of body size reduction occurred through different  
274 processes in mainland and island species. For example, mainland taxa went from two body size  
275 peaks to a single size peak, and island taxa moved from a left-skewed distribution to a uniform  
276 distribution in body size. The difference in timing of extinctions between mainland and islands  
277 has been attributed to the delayed arrival of humans on islands matching with the geographic  
278 extirpation patterns of tortoises [14], whereas discrepancies in body size patterns between  
279 mainland and island ecosystems might be due to specific habitats and associated changes  
280 [61,70]. Body size transitions such as those found here for tortoises have also been observed in  
281 terrestrial mammals following the late Quaternary extinctions [49,71]. However, general trends in  
282 the distribution of body sizes of insular mammals differ from those of insular tortoises [72], with  
283 insular mammals having mostly multimodal and right-skewed distributions [72]. The prevailing  
284 explanation for this pattern is that (herbivore) mammals generally adhere to the island size rule  
285 where small animals evolve larger body size on islands and vice versa [73]. Body size patterns  
286 of extant tortoises, i.e. larger species on islands than on the mainland, also seem to follow the  
287 island rule. However, biogeographic studies on dispersal patterns of tortoises and consideration  
288 of the fossil record have revealed that large-bodied taxa evolved on the mainland and later

289 dispersed to islands where they became even larger, therefore contradicting the island rule  
290 [32,74]. The later extinction of all large-bodied tortoises on the mainland and almost all large-  
291 bodied tortoises in islands generated the body size pattern present in extant taxa [14].

292 The overall reduction in body size of extant turtles resulted in the homogenization of ecological  
293 functions, with potential severe consequences for ecosystems [9]. Multiple studies have shown a  
294 major role for larger-bodied animals providing important ecosystem services [3,4,13]. For  
295 example, giant tortoises are recognized to maintain ecosystems through grazing, browsing,  
296 trampling, selective feeding, nutrient cycling, and seed dispersal [7,9,10]. Observational data  
297 suggests that smaller-sized animals can also be effective seed dispersers [75–79] and large size  
298 does not necessarily result in longer gut retention time [80]. However, megaherbivores play a  
299 more important role in this regard compared to smaller animals because they usually consume  
300 larger amounts of food and thereby seeds, can eat larger fruits, exploit a larger area and move  
301 over longer distances [3–6]. For example, the loss of mammalian megaherbivores has been  
302 associated with changes in plant communities, vegetation structure, biome shifts, fire activity,  
303 and nutrient cycling [3,4,6]. Similarly, the disappearance of endemic, large tortoises on the  
304 Galápagos islands has resulted in the loss of wetland habitats [9]. The impact of the recent  
305 extinction of giant tortoises is so severe that rewilding programs with non-native extant giant  
306 tortoises have been developed to restore these lost ecosystem services [9,10]. While we can  
307 estimate the effect of giant tortoise extinctions on island ecosystems with some precision given  
308 that some taxa still remain and several extinctions are rather recent, the ecological impacts of  
309 giant tortoise extinctions on continents are less clear. Mainland tortoises were disproportionately  
310 affected by the extinction of megafaunal taxa with the eradication of all giant taxa on continents  
311 [14]. Mainland giant tortoises were not the largest herbivores in their respective communities and  
312 their ecological functions were shared with mammalian megafauna [13] in contrast to insular  
313 taxa, making giant tortoises on islands potentially less redundant and therefore more unique  
314 ecosystem engineers than on the mainland. Regardless of whether or not giant tortoises played

315 unique ecological roles on the mainland, the sheer extent of their extinction in conjunction with  
316 mammalian megafauna extinctions likely altered ecosystem functioning [3,13].

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

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528 **Figure legends**

529 **Figure 1:** A) Body size distribution of all tortoises is bimodal and right-skewed: small body sizes  
530 are the most frequent. B) Temporal comparison of body size distribution shows extant and fossil  
531 taxa are both bimodal and right-skewed: small body sizes are more frequent than large body  
532 sizes. Body size overlap is high between fossil and extant tortoises. C) Spatial comparison of  
533 body size distribution shows it is right-skewed and bimodal in mainland tortoises while it is left-  
534 skewed and bimodal in insular tortoises. Body size overlap is low between mainland and insular  
535 tortoises because of the contrasting skew. D) Left: Body size distribution of extant taxa on  
536 islands is rather uniform. Body size distribution of fossil taxa on islands is unimodal and, in  
537 contrast to all other groups, left-skewed: large body sizes are the most frequent. Body size  
538 overlap is low between fossil and extant tortoises in islands. Right: Body size distribution of  
539 mainland tortoises is right-skewed for extant and fossil taxa and bimodal for fossil tortoises but  
540 unimodal for extant tortoises due to lack of large-bodied taxa. Body size overlap is high between  
541 fossil and extant tortoises on the mainland due to the preserved cluster of small-bodied taxa.

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

550 **Figure 3:** Evolutionary trajectory of straight carapace length (SCL) over time for A) all taxa, B)  
551 mainland taxa, and C) island taxa. Points and bars represent the mean carapace length within  
552 each time bin and standard errors, respectively. Black dashed line depicts the mean carapace

553 length averaged across all time bins. Grey background indicates the different epochs: from the  
554 Miocene over the Pliocene to the Pleistocene (from light to dark). Letters indicate the  
555 stratigraphic stages from the Miocene to the Recent( B/A = Burdigalian/Aquitanian, L =  
556 Langhian, S = Serravallian, T = Tortonian, M = Messinian, Z = Zanclean, P = Piacencian, G =  
557 Gelasian, EP = Early Pleistocene, MP = Middle Pleistocene, LP = Late Pleistocene, R =  
558 Recent). Body size increases consistently until the Late Miocene (Messinian), briefly dips and  
559 rises again in the Pliocene and then steadily drops with onset of the Pleistocene for all tortoises  
560 and mainland tortoises. The oldest and largest island tortoises are known from the Late Miocene  
561 and also experience a dip and subsequent rise during the Pliocene and then drop during the  
562 Pleistocene.

563 **Tables**

564 *Table 1: Descriptive statistics of straight carapace length (SCL) for the entire data set (all) as well as different subgroups, i.e. per time*  
 565 *bin (min - max Ma), extant and fossil tortoises, mainland and insular taxa in general and for extant and fossil tortoises separately. The*  
 566 *table contains sample size (Individuals), number of species (Species), number of genera (Genera), minimum, maximum, mean, median,*  
 567 *variance, skewness, kurtosis, as well as the corresponding log values of straight carapace length. Time ranges, mean age per bin,*  
 568 *corresponding stratigraphic stages and epochs, and respective sample sizes (on individual, species and genus level). Apart from the*  
 569 *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	Mean SCL	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	164134.09	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	67449.64	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	68527.81	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	97470.85	3.03	12.2	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	161825.86	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	407449.36	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	274229.86	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	478925.31	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	552706.72	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	172995.44	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	159888.34	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	235193.56	0.29	1.52	6.4	6.4	0.04	1.16

Burdigalian/Aquitani an (15.97-23.03 Ma)	36	16	10	113.0	1100	372.1	273.3	69970.94	1.44	4.05	5.7	5.6	0.53	2.37
Fossil	378	116	24	90.0	2500	505.0	285.4	216559.77	1.84	6.16	5.9	5.7	0.66	2.43
Insular	147	56	19	80.0	2000	578.0	500.0	159787.40	1.01	3.94	6.1	6.2	-0.28	2.06
Mainland	483	129	29	81.0	2500	391.1	250.0	157622.64	2.64	10.4	5.7	5.5	1.05	3.70
										9				
Extant insular	96	32	12	80.0	1300	471.3	353.0	118529.81	0.82	2.48	5.9	5.9	0.01	1.77
Extant mainland	156	41	15	81.0	830	241.9	221.0	16402.64	1.97	8.58	5.4	5.4	0.29	3.01
Fossil insular	51	26	10	150.0	2000	778.9	750.0	178351.30	1.11	4.06	6.5	6.6	-0.37	3.14
Fossil mainland	327	98	24	90.0	2500	462.3	270.0	209518.11	2.11	7.29	5.8	5.6	0.93	2.96

570

571 *Table 2: Model-fitting results for the complete data set as well as mainland and insular subsets comparing three models (GRW =*  
 572 *Generalized Random Walk, Unbiased Random Walk, and Stasis). Stasis is the best supported model (largest Akaike weights in bold) for*  
 573 *all three data sets with the highest model support for insular data.*

Data	Model	Log Likelihood	K	AICc	Akaike Weight
	Stasis	-71.71	2	148.9	<b>0.851</b>
All	URW	-75.36	1	153.2	0.103
	GRW	-74.63	2	154.8	0.046
	Stasis	-74.9	2	155.3	<b>0.708</b>
Island	URW	-77.72	1	157.9	0.195
	GRW	-76.89	2	159.3	0.097
	Stasis	-52.73	2	112.5	<b>0.941</b>
Mainland	URW	-123.9	1	250.5	0.000
	GRW	-55.51	2	118	0.059

574

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578 **Author contributions**

579 J.M. and D.B.M conceptualized the project; J.J. collected and curated the data; J.J. and C.P.  
580 analyzed the data; J.J. wrote the manuscript with contributions from J.M., C.P. and D.B.M.

581 **Data accessibility**

582 The datasets supporting this article have been uploaded as part of the supplementary material.

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585 **Competing interests**

586 We declare we have no competing interest.