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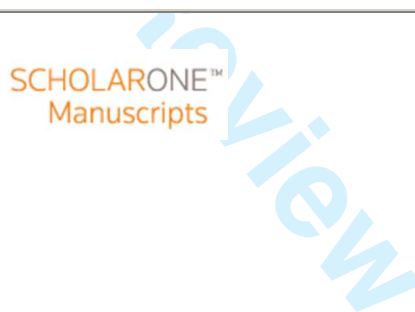


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**Late Quaternary reptile extinctions: size matters, insularity dominates**

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3 **1 Late Quaternary reptile extinctions: size matters, insularity dominates**

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30 Quaternary; reptiles

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3 **21 ABSTRACT**  
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6 **22 Aim** A major Late Quaternary vertebrate extinction event affected mostly large-sized  
7 'megafauna'. This is well documented in both mammals and birds, but evidence of a  
8 similar trend in reptiles is scant. We assess the relationship between body size and  
9 Late Quaternary extinction in reptiles at the global level.  
10  
11

12  
13 **26 Location** Global.  
14  
15

16 **27 Methods** We compile a body size database for all 82 reptile species that are known  
17 to have gone extinct during the last 50,000 years and compare them to the sizes of  
18 10,090 extant reptile species (97% of known extant diversity). We assess the body  
19 size distributions in the major reptile groups: crocodiles, lizards, snakes, and turtles,  
20 while testing and correcting for a size-bias in the fossil record. We examine  
21 geographical biases in extinction by contrasting mainland and insular reptile  
22 assemblages, and testing for biases within regions and then globally by using  
23 geographically weighted models.  
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31 **35 Results** Extinct reptiles were larger than extant ones, but there was considerable  
32 variation in extinction size-biases among groups. Extinct lizards and turtles were  
33 large, extinct crocodiles were small, and there was no trend in snakes. Lizard  
34 lineages vary in the way their extinction is related to size. Extinctions were  
35 particularly prevalent on islands, with 73 of the 82 extinct species being island  
36 endemics. Four others occurred in Australia. The fossil record is biased towards  
37 large-bodied reptiles, but extinct lizards were larger than extant ones even after we  
38 account for this.  
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46 **43 Main conclusions** Body size played a complex role in the extinction of Late  
47 Quaternary reptiles. Larger lizard and turtle species were clearly more affected by  
48 extinction mechanisms such as over exploitation and invasive species, resulting in a  
49 prevalence of large-bodied species among extinct taxa. Insularity was by far the  
50 strongest correlate of recent reptile extinctions, suggesting size-biased extinction  
51 mechanisms are amplified in insular environments.  
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## 49 INTRODUCTION

50 Body size represents one of the most identifiable traits of an organism and is closely  
51 tied to its functional ecology, life-history, morphology and physiology (Peters, 1983).  
52 Size has also been strongly implicated in species' extinction risk (Diamond, 1984;  
53 Case *et al.*, 1998; Dirzo *et al.*, 2014). As evidence is accumulating that the planet is  
54 experiencing a mass extinction event, rivalling those of the geological past (Barnosky  
55 *et al.*, 2011; Maclean & Wilson, 2011; Barnosky *et al.*, 2012; Ceballos *et al.*, 2015),  
56 increasing attention is being paid to the factors responsible for this decline in  
57 biodiversity (e.g., Purvis *et al.*, 2000; Cardillo *et al.*, 2005; Brook *et al.*, 2008). Traits  
58 associated with increased vulnerability to extinction include habitat specialisation,  
59 small geographic range, insularity, and those associated with slow life-histories such  
60 as low reproduction rates, late maturity, low population densities and large body  
61 size (Owens & Bennett, 2000; Cardillo *et al.*, 2006; Tingley *et al.*, 2013). During the  
62 last 50,000 years anthropogenic pressure is purported to have elevated vertebrate  
63 extinction rates far beyond the normal background level (Ceballos *et al.*, 2015).

64 Evidence from the Late Quaternary fossil record has revealed the extinction of a  
65 considerable array of vertebrates across the globe, particularly among the large-  
66 bodied species (Martin & Klein, 1984; Brook & Bowman, 2002; Sandom *et al.*, 2014).  
67 During this period Eurasia and North America lost c. 36% and 72% of their large-  
68 bodied mammalian genera, respectively (Barnosky *et al.*, 2004). Twenty-three  
69 mammalian species > 10 kg, distributed across 15 genera, also vanished from the  
70 Australian fauna during the same time (Sandom *et al.*, 2014). This period further  
71 coincides with the extinction of the world's largest birds, the Madagascan elephant  
72 birds and New Zealand moas (~7 spp. and ~10 spp. respectively, Mitchell *et al.*,  
73 2014). While the extinction wave was not exclusively restricted to megafauna  
74 (Owens & Bennett, 2000), and taphonomic size-biases in the fossil record may be  
75 partially obscuring the exact trend (Damuth, 1982), most extinct species were indeed  
76 large. Large body size is correlated with slow life-history traits, and is strongly  
77 implicated in current species extinction risk (Cardillo *et al.*, 2005; Fritz *et al.*, 2009).  
78 The Late Quaternary reptile fossil record is poorly known compared to birds and  
79 mammals, perhaps because there are few late-Cenozoic reptile paleontologists,

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2  
3 80 especially in tropical countries where reptiles tend to occur high in numbers. Yet,  
4  
5 81 several of the extinct reptile species, such as the Australian *Wonambi naracoortensis*  
6  
7 82 (snake), *Meiolania* sp. (tortoise), and *Varanus priscus* (lizard) were huge by current  
8  
9 83 standards (Wroe, 2002; Conrad *et al.*, 2012; Rhodin *et al.*, 2015).

10  
11 84 The loss of a considerable portion of the planet's megafauna during the Late  
12  
13 85 Quaternary has sparked intense debate over the possible extinction mechanisms  
14  
15 86 (Martin & Klein, 1984; Flannery, 1999; Johnson, 2006; Koch & Barnosky, 2006; Wroe,  
16  
17 87 2006; Johnson *et al.*, 2016). Many studies have focused on contrasting the biological  
18  
19 88 traits between extinct and extant species (e.g., Johnson, 2002; Lorenzen *et al.*, 2011),  
20  
21 89 and body size has often emerged as a key factor. Size-biased extinction has  
22  
23 90 predominantly been identified in mammals, with the global loss of over 150 large  
24  
25 91 mammalian species ( $\geq 44$  kg in body size) since the last interglacial (Sandom *et al.*,  
26  
27 92 2014). The bird fossil record is not as well known, but nonetheless over 1,000 mostly  
28  
29 93 large bodied species are estimated to have gone extinct during this time, many of  
30  
31 94 them flightless, insular endemics (Duncan *et al.*, 2013). The proximate causes of  
32  
33 95 extinction among birds and mammals have been attributed to direct and indirect  
34  
35 96 anthropogenic pressure and climate change (Ceballos *et al.*, 2015; Johnson *et al.*,  
36  
37 97 2016). Few studies have investigated size-bias trends and extinction mechanisms in  
38  
39 98 Quaternary reptiles (but see Pregill, 1986; Kemp & Hadly, 2015). As current trends  
40  
41 99 suggest that the reptile extinction rate is much higher than expected (Alroy, 2015),  
42  
43 100 studies focusing on their extinction mechanisms are both timely and important.

44  
45 101 Reptiles are one of the most species-rich land vertebrate groups (~10,400 species;  
46  
47 102 Uetz & Hosek, 2016), and are the most poorly represented in conservation  
48  
49 103 prioritization (Böhm *et al.*, 2016). Reptile traits associated with increased extinction  
50  
51 104 risk include restricted geographic range, habitat specificity and large body size  
52  
53 105 (Tingley *et al.*, 2013; Kemp & Hadley, 2015). Although extant large bodied reptiles  
54  
55 106 are purportedly more prone to extinction, this may have arisen due to a size-bias in  
56  
57 107 reptile assessments (Meiri, 2008). The sheer paucity of data on reptile distributions,  
58  
59 108 population trends, life-history, and fossil record has thus far precluded a  
60  
109 comprehensive, taxon-wide assessment of their extinction risk correlates (Böhm *et*  
110 *al.*, 2016).

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2  
3 111 To better understand the threats faced by current extant reptiles, elucidating the  
4 112 past trends and processes responsible for recent extinction events is of crucial  
5 113 importance (Barnosky *et al.*, 2004). Paleontological and archaeological records of  
6 114 Holocene reptile extinctions, although incomplete, provide an invaluable resource  
7 115 for identifying these factors (Pregill & Dye, 1989). Fossil evidence has revealed recent  
8 116 extinctions among several reptile lineages across the globe, and their disappearance  
9 117 is invariably attributed to human impact (e.g. Pregill, 1991; Hedges & Conn, 2012;  
10 118 Rhodin *et al.*, 2015). Estimations of body size also indicate that many of these  
11 119 reptiles, particularly from insular assemblages, were unusually large compared to  
12 120 their extant kin (Pregill, 1986; Kemp & Hadly, 2015).

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21 121 To determine whether reptiles exhibit size-biased extinction, we assess body size  
22 122 distributions among extinct and extant assemblages across the globe. Body size of  
23 123 reptiles (and indeed, all animals) is shaped by many factors including phylogeny,  
24 124 geography and different adaptive regimes. Where feasible, we therefore assess the  
25 125 size-bias trend across multiple taxonomic levels and geographic regions.

## 30 31 126 **METHODS**

### 32 33 34 127 **DATA COLLECTION**

35  
36  
37 128 We collected data on the maximum body size of all 82 reptile species that went  
38 129 extinct since humans colonized their range (Table S1 in Supporting Information).  
39 130 These include four crocodile, 45 lizard, 9 snake and 24 turtle ('turtles' here refers to  
40 131 all members of the order Testudines) species. We scoured published sources  
41 132 including books, assessments by the International Union for the Conservation of  
42 133 Nature (IUCN) and the primary literature to determine the identities and body sizes  
43 134 of extinct reptile species. We considered species to be extinct if they are known only  
44 135 from fossils, or were declared extinct by the IUCN or in the primary literature, and if  
45 136 their extinction happened following human occupation of their range (~50,000 years  
46 137 for Australia, ~14,000 years for the Americas, ~3,000 years for Oceania, and ~2,000  
47 138 years for Madagascar; Barnosky *et al.*, 2004; Burney *et al.*, 2004; Anderson, 2009).  
48  
49 139 We compare these to the body sizes of 10,090 extant species we collected from  
50  
51  
52  
53  
54  
55  
56 140 published accounts (189 amphisbaenians, 24 crocodiles, 6045 lizards, 3513 snakes,  
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3 141 318 turtles and the one species of tuatara; Table S2 in Supporting Information). We  
4  
5 142 converted all length data to masses using family and clade-specific length-mass  
6  
7 143 allometric equations (Table S1). This is crucial as length is an inadequate measure of  
8  
9 144 body size to compare across taxa with highly variable body shapes (Feldman & Meiri,  
10  
11 145 2013). A list of all data sources is found in Appendix 1.

12  
13 146 We also collected distribution data on all extant and extinct species in order to take  
14  
15 147 into account geographical patterns in extinctions of reptiles. Data on extant species  
16  
17 148 were obtained from GARD (Global Assessment of Reptile Distributions; 2015),  
18  
19 149 whereas data on extinct species were collected from the same sources as the body  
20  
21 150 size data (listed in Table S1).

22  
23 151 We classified each species as either an insular endemic or not, and assigned each  
24  
25 152 species to a biogeographical realm. We used ArcGIS 10.0 (ESRI) to project shapefiles  
26  
27 153 of reptile species distributions onto a map of biogeographical realms (Wallace,  
28  
29 154 1876). A species was assigned to a realm if all or the largest part of its distribution  
30  
31 155 area fell inside that realm. A species was designated insular endemic if no part of its  
32  
33 156 range overlapped with a continental landmass (therefore, we considered islands as  
34  
35 157 any landmass smaller than Australia, the largest island with reptiles being New  
36  
37 158 Guinea).

38  
39 159 We also collected data on occurrence of extant species of reptiles in the fossil record  
40  
41 160 to test for size-biases in the fossil record. We searched in FossilWorks  
42  
43 161 (<http://www.fossilworks.org>) and Google Scholar using the keywords “Holocene”,  
44  
45 162 “Late Pleistocene”, “Squamata”, and “Reptilia”, as well as in two books on the  
46  
47 163 Pleistocene herpetofaunas of North America and Europe (Holman, 1995; 1998), and  
48  
49 164 collected data on the occurrence of 261 extant species of reptiles in the fossil record  
50  
51 165 (4 amphisbaenians, 9 crocodiles, 94 lizards, 105 snakes, 48 turtles and the one  
52  
53 166 species of tuatara; Table S2).

## 54 55 167 **PERMUTATION TESTS**

56  
57 168 Reptile size distributions are strongly right skewed (Feldman *et al.*, 2016), breaking  
58  
59 169 the assumption of normality required for parametric statistical tests. Thus, we  
60

1  
2  
3 170 conducted permutation tests to compare body sizes of extant and extinct species.  
4  
5 171 This was done (for all reptiles and separately for lizards, snakes, turtles and  
6  
7 172 crocodiles) by pooling all extant and extinct species of each group, randomly  
8  
9 173 selecting  $n$  species from the pool without replacement (where  $n$  is the observed  
10  
11 174 number of extinct species within the examined taxon e.g.,  $n = 45$  for lizards), and  
12  
13 175 computing the t-statistic for the random selection using the formula:

14  
15 176 
$$t_i = \frac{\mu_{extinct} - \mu_{extant}}{SE_{extinct}}$$

16  
17 177 Where  $\mu_{extinct}$  is the mean body size of the random selection (simulated extinct  
18  
19 178 species),  $SE_{extinct}$  is the standard error of the random selection, and  $\mu_{extant}$  is the mean  
20  
21 179 body size of the remaining, non-selected species in the pool (simulated extant  
22  
23 180 species). This process was repeated for 100,000 iterations. Using the same formula  
24  
25 181 we computed a t-statistic for the observed extinct and extant groups, and computed  
26  
27 182 two sided p-values as the fraction of iterations with t-statistics at least as extreme as  
28  
29 183 the observed value (with  $\alpha = 0.05$ ).

#### 30 184 **FOSSIL RECORD BIASES**

31  
32  
33 185 Due to the incompleteness of the fossil record, the results of our analyses might be  
34  
35 186 biased if the sample size of extinct species is too low. This is of special concern as  
36  
37 187 large-bodied taxa are more likely to be preserved (Damuth, 1982). To account for  
38  
39 188 this, we performed rarefaction analyses. We randomly sampled 80%, 60%, 30% and  
40  
41 189 10% of the total extinct species (in each taxon) and ran the permutation tests (with  
42  
43 190 only 10,000 iterations to reduce computational time) on these subsets. This sampling  
44  
45 191 process was repeated 1,000 times to generate rarefaction curves. We then  
46  
47 192 examined, for each curve, at which sampling effort do the results of the permutation  
48  
49 193 tests become non-significant, i.e. the minimum sampling required to achieve  
50  
51 194 significance. This test informed us of the robustness of our analyses to low sample  
52  
53 195 sizes due to missing data in the fossil record.

54  
55 196 The fossil record itself may also be size-biased due to taphonomic issues, because  
56  
57 197 larger bones have a higher chance to be preserved due of their low surface area to  
58  
59 198 volume ratio (Damuth, 1982). We tested for this size-bias by comparing the body  
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3 199 sizes of extant reptile species that occur in the fossil record to all extant species. We  
4  
5 200 performed permutation tests as described above for all reptiles, and separately for  
6  
7 201 lizards, snakes, crocodiles, and turtles. Furthermore, we repeated our analyses of  
8  
9 202 size-bias in extinct lizards after excluding all extinct species that are known only from  
10  
11 203 fossils or sub-fossils (e.g., *Varanus priscus*). As this analysis only included a subset of  
12  
13 204 species that went extinct after living specimens had been collected and scientifically  
14  
15 205 described (28 species; e.g. *Ameiva cineracea*), rather than preserved remains, it  
16  
17 206 should not be affected by a size-bias in the fossil record.

### 18 207 **GEOGRAPHICAL BIASES**

19  
20  
21 208 Late Quaternary reptile extinctions are heavily biased towards islands (Fig. 1). If  
22  
23 209 insular species differ in body size from mainland species, observed size-biases in  
24  
25 210 extinct taxa may simply reflect insular size-biases (i.e. if island reptiles are unusually  
26  
27 211 large, then extinct reptiles would be larger than extant ones simply because insular  
28  
29 212 species went extinct more often). To test whether extinction rates are indeed higher  
30  
31 213 on islands, we performed Fisher exact tests with a null hypothesis of identical  
32  
33 214 extinction frequencies for both mainland species and insular endemics. We then  
34  
35 215 tested exclusively among extant species whether insular endemics are larger than  
36  
37 216 mainland species using permutation tests as described above (with  $n$  representing  
38  
39 217 the number of insular species). Furthermore, we examined whether an extinction  
40  
41 218 size-bias existed among insular endemic species only. This could not be performed  
42  
43 219 for mainland species due to the extreme scarcity of extinct mainland reptiles we  
44  
45 220 have data for (see Results).

46  
47 221 Reptile extinctions are also clearly geographically biased (Fig. 1). To account for  
48  
49 222 different geographical patterns in reptile extinctions, we used two approaches. First,  
50  
51 223 we performed geographically weighted permutation analyses. This was carried out  
52  
53 224 using the permutation analyses as described above, but with a species selection  
54  
55 225 probability from the pool dependent upon its biogeographical realm (i.e. the  
56  
57 226 probability of selecting a species was proportional to the number of extinct species  
58  
59 227 in its realm divided by the global number of extinct species). This ensured that each  
60  
61 228 simulated extinct selection had the same distribution of realms as the observed

1  
2  
3 229 distribution of extinct species. We conducted these analyses for all reptiles and for  
4  
5 230 lizards, snakes, and turtles separately. Crocodiles were omitted because, of the three  
6  
7 231 realms in which there were extinct crocodiles, Oceania and Madagascar have no  
8  
9 232 extant species.

10  
11 233 Second, we ran permutation tests on three regional assemblages to determine  
12  
13 234 whether the global patterns are comparable across varying spatial scale. As only a  
14  
15 235 few regions contained a sufficient number of extinct reptiles we only ran three such  
16  
17 236 analyses: Caribbean lizards (31 extinct and 377 extant species), Mascarene lizards (5  
18  
19 237 extinct and 19 extant species), and Galapagos tortoises (*Chelonoidis* spp., 3 extinct  
20  
21 238 and 7 extant species).

### 22 239 **PHYLOGENETIC BIASES**

23  
24  
25 240 Finally, we examined whether the size-biases in extinct reptilian taxa were  
26  
27 241 phylogenetically skewed. We ran permutation tests on all reptile families (Dipsadidae,  
28  
29 242 Gekkonidae, Iguanidae, Lacertidae, Leiocephalidae, Scincidae, Teiidae, and  
30  
31 243 Testudinidae) and genera (*Alinea*, *Ameiva*, *Chelonoidis*, *Hypsirhynchus*, *Leiocephalus*,  
32  
33 244 *Leiopisma*, *Mabuya*, *Phelsuma*, *Spondylurus*) that include more than one extinct  
34  
35 245 and one extant species.

36  
37 246 All statistical analyses were performed in R v3.2.0 (R Development Core Team,  
38  
39 247 2015).

### 40 248 **RESULTS**

41  
42  
43 249 Most of the extinct reptile species were insular endemics (Fig. 1), with a remarkably  
44  
45 250 large concentration of extinct species in the Caribbean. Notable extinctions also  
46  
47 251 occurred on the Mascarene, Galapagos, Melanesian, and Polynesian islands.  
48  
49 252 Relatively few reptiles (mostly turtles) went extinct in mainland regions, mostly in  
50  
51 253 Australia. Eurasia is the only continental landmass from which no extinct reptiles  
52  
53 254 from the Late Pleistocene to Holocene are known, while Africa and South America  
54  
55 255 had one extinction each.  
56  
57  
58  
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1  
2  
3 256 Results of the permutation analyses are presented in Table 1. Across all reptiles  
4  
5 257 there was a significant extinction size-bias. The vast majority of extant reptiles are  
6  
7 258 small, whereas extinct species were disproportionately large (Fig. 2). A similar pattern  
8  
9 259 is also evident in the most species-rich reptilian taxon (co-incidentally the one  
10  
11 260 suffering most extinctions): the lizards. Extinct lizards were nine times larger than  
12  
13 261 extant lizards (Fig. 3a). This was also true for the Caribbean lizard assemblage, but it  
14  
15 262 was not significant in the Mascarene lizard assemblage, despite extinct species being  
16  
17 263 twice as large as extant ones (Table 1). Extinct turtles were 16-times larger than  
18  
19 264 extant turtles (Fig. 3c). Interestingly, this was not true for the Galapagos tortoise  
20  
21 265 assemblage. Surprisingly, extinct Galapagos tortoises were similar in size to extant  
22  
23 266 ones. Unlike lizards and turtles, extinct crocodiles were significantly smaller than  
24  
25 267 extant crocodiles (Fig. 3d). Finally, while extinct snakes were twice as large as extant  
26  
27 268 snakes (Fig. 3b), this difference is not statistically significant (Table 1). All the  
28  
29 269 observed differences between extinct and extant species held when our analyses  
30  
31 270 were geographically weighted (Table 1).

32  
33 271 The reptile fossil record is size-biased (Fig. 2). Size-biases are evident in the fossil  
34  
35 272 records of lizards and snakes, with the species present in the fossil record  
36  
37 273 representing a large-bodied subset of extant species. No such bias was detected in  
38  
39 274 the fossil records of either turtles or crocodiles (Table 1). When we omitted extinct  
40  
41 275 species known only from the fossil record from our analysis, we still detected a size-  
42  
43 276 bias: extinct lizards were four times larger than extant ones (Table 1).

44  
45 277 The results of the rarefaction analyses on lizards and turtles (snakes and crocodiles  
46  
47 278 were not analysed because their low sample size prohibited reduced sampling)  
48  
49 279 indicate that our permutation analyses are robust despite the incompleteness of the  
50  
51 280 fossil record. In both lizards and turtles, the median minimum sampling effort  
52  
53 281 required to achieve significance, out of 1,000 repetitions, was 60%. This means that  
54  
55 282 we would get an equivalent pattern with little more than half the sampling effort we  
56  
57 283 actually achieved.

58  
59 284 Reptile extinction events were remarkably prevalent on islands. Seventy three of the  
60  
61 285 82 extinct species (89%) were insular endemics ( $p < 0.01$  for lizards, snakes and



1  
2  
3 286 turtles,  $p = 0.02$  for crocodiles; Fig. 4) while only 26% of extant species are insular.  
4  
5 287 When mainland species are excluded from the analyses, removing the confounding  
6  
7 288 effects of size differences between island and mainland species, all the observed  
8  
9 289 size-biases still appear (Table 1). Even the inclusion of mainland species does not  
10  
11 290 change the pattern. Furthermore, the body size differences between insular  
12  
13 291 endemics and mainland species do not reflect the size differences between extinct  
14  
15 292 and extant species (Table 1). Extant insular endemic lizards and snakes are  
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17 293 significantly smaller than mainland species. Insular crocodylians are similar in size to  
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19 294 mainland ones. Only in turtles are insular species larger than mainland species (see  
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21 295 also Itescu *et al.*, 2014), but the difference is not nearly as large as between extinct  
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23 296 and extant species. Therefore, large lizards and turtles, and small crocodiles, went  
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25 297 extinct regardless of whether they were on islands or on the mainland.

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27 298 The global patterns were not always reflected at the family and genus levels. Extinct  
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29 299 Dipsadid snakes, Leiocephalid and Scincid lizards, and Testudinid turtles were larger  
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31 300 than extant ones (Table 1; Fig. 5a). Four families (Gekkonidae, Iguanidae, Lacertidae,  
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33 301 and Teiidae) showed no significant trends. Of nine genera tested only *Leiocephalus*  
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35 302 (the sole genus in Leiocephalidae) showed a significant size-bias (Fig. 5b), although in  
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37 303 some genera and families there may be an issue of statistical power due to low  
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39 304 sample sizes (Table 1).

## 38 305 **DISCUSSION**

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41 306 The global extinction of the Late Quaternary vertebrate megafauna indicates body  
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43 307 size may have played a pivotal role in recent extinction events. We find that recently  
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45 308 extinct reptiles were much larger than extant ones. Size-biases, however, differ  
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47 309 across the four major reptile groups. Extinctions were biased towards large lizards  
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49 310 and turtles, and small crocodiles, while there was no significant size-bias in snakes.  
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51 311 Our results also suggest that the observed size-bias in extinct lizards is not general  
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53 312 across clades, but is phylogenetically skewed and driven by the largest members of  
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55 313 only a few clades that have gone extinct (e.g., *Leiocephalus* spp., a large skink,  
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57 314 *Chioninia coctei*, and the largest gecko, *Hoplodactylus delcourti*, and lizard, *Varanus*  
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59 315 *priscus*, to have ever lived). Our analyses may have been conservative, as we used  
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3 316 the maximum size reported for each species, regardless of whether it was measured  
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5 317 in extant populations or estimated from sizes of subfossil conspecifics. In many  
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7 318 extant taxa (e.g., *Gallotia stehlini*, *G. bravoana*, *Chioninia vaillantii*, *Diploglossus pleii*,  
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9 319 *Anolis cuvieri*, see e.g., Pregill, 1986) these maximum sizes were estimated for  
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11 320 recently extinct populations, and living members are much smaller. Small sample  
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13 321 sizes of extinct taxa may also mask their true size maxima, making them appear  
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15 322 smaller than they really were (Meiri, 2007).

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17 323 Comprehensive assessments of the reptile fossil record remain sparse, and worse;  
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19 324 most reptiles are and were small-bodied (Feldman et al., 2016). Hence, their bones  
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21 325 are often badly preserved or missed altogether, making species-level identification  
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23 326 impossible in many cases. This may cause a possible bias in favour of large-bodied  
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25 327 species in the fossil record (Damuth, 1982). Indeed, we found evidence of such a bias  
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27 328 – extant species that are represented in the fossil record are roughly seven times  
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29 329 larger than the mean size of all extant species. However, *extinct* is not the same as  
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31 330 *fossil*, and many extinct species are known from intact, well-preserved museum  
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33 331 specimens for which no taphonomic effect is imaginable. When we omitted extinct  
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35 332 species only known from fossils or sub-fossils from our analyses, and only examined  
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37 333 species that were collected alive prior to their extinction (and therefore suffer from  
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39 334 no taphonomic biases), we still managed to detect a size-bias towards larger extinct  
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41 335 lizard species. Furthermore, some of our uncovered patterns (e.g., small extinct  
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43 336 crocodiles, similarly sized extinct snakes) cannot be explained by such a bias. Despite  
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45 337 the apparent robustness of our results to taphonomic bias, we advise caution  
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47 338 whenever analyses of body sizes of extinct species are attempted, and a size-bias in  
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49 339 the fossil record must be tested and corrected for.

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51 340 Both intrinsic life-history traits and extrinsic factors such as climate change and  
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53 341 anthropogenic pressure are linked to species survival (Brook *et al.*, 2008). Cardillo *et*  
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55 342 *al.* (2005) found that small mammals' (< 3 kg) are threatened by environmental  
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57 343 factors, while larger mammals are threatened by a combination of extrinsic  
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59 344 environmental factors and intrinsic biological traits. These factors are purported to  
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345 act in synergy, whereby the simultaneous action of separate processes have a  
346 stronger effect than the sum of individual effects (Brook *et al.*, 2008). In lizards, we

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3 347 find evidence that larger species may indeed have been more susceptible to  
4 348 extinction, as 38 of the 45 extinct lizards were larger than the extant mean of 9.5 g,  
5 349 19 of them being over an order of magnitude larger. Kemp & Hadly (2015) recently  
6 350 reported a size-bias in Caribbean lizard species with extinction probability increasing  
7 351 with body size. They concluded that larger sized lizards with 'slower' life-histories  
8 352 were more prone to extinction due to environmental change and anthropogenic  
9 353 pressure, factors purported to increase in intensity on islands. Further research is  
10 354 required to elucidate whether a precise mass threshold exists, and if present,  
11 355 identify the underlying extinction mechanisms. Such extinction mechanisms may be  
12 356 particularly insightful considering large lizards typically lay larger, rather than smaller  
13 357 clutches (Bauwens & Diaz-Uriarte 1997; Meiri *et al.*, 2012), thus low fecundities are  
14 358 unlikely to have triggered extinctions.

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17 359 While it is evident that recent extinction events can rarely be attributed to a single  
18 360 cause (Didham, 2005), emergent trends implicate the fundamental role of both  
19 361 direct and indirect anthropogenic pressure (Davies *et al.*, 2006; Koch & Barnosky,  
20 362 2006; Dirzo *et al.*, 2014; Johnson *et al.*, 2016). Direct evidence of human-mediated  
21 363 extinction among reptiles is documented in the over-harvesting of giant iguanas on  
22 364 Southwest Pacific islands (Pregill & Steadman, 2004) and giant tortoises in the  
23 365 Caribbean, Indian Ocean and Pacific Ocean islands (Rhodin *et al.*, 2015). It is evident  
24 366 that humans targeted these large bodied reptiles precisely because their size  
25 367 represented a substantial source of nutrition, whilst their lack of defence  
26 368 mechanisms reduced the risk taken during their capture. Interestingly, our study  
27 369 indicates that among the Galapagos giant tortoises, the extinct species were not the  
28 370 largest members of the assemblage, and in fact many larger species (*Chelonoidis*  
29 371 *becki*, mass = 154 kg; *C. vicina*, mass = 249 kg; and *C. nigra*, mass = 277 kg) still  
30 372 survive to this day. Similarly, the sole remaining extant giant tortoise in the Western  
31 373 Indian Ocean (*Aldabrachelys gigantea*, mass = 217 kg) is the second largest species  
32 374 within this assemblage following the extinct *Cylindraspis indica* (mass = 222 kg). It  
33 375 may be that these smaller giant tortoise species may have been preferentially  
34 376 targeted by 18<sup>th</sup> century sailors due to ease of transport, resulting in their eventual

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3 377 extinction (Hansen *et al.*, 2010), while the larger species proved to be more of a  
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5 378 handful.

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8 379 For crocodiles and snakes, the extinction mechanisms and role of body size are  
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10 380 harder to pinpoint. Two of the four extinct crocodiles (*Mekosuchus inexpectatus* and  
11 381 *Volia athollandersoni*) were confined to Pacific islands (Molnar *et al.*, 2002). While  
12 382 this undoubtedly increased their extinction vulnerability, evidence for direct hunting  
13 383 by humans, as in the case of the Pacific meiolaniid tortoises, is lacking (Molnar *et al.*,  
14 384 2002). In the case of the Madagascan crocodile (*Voay robustus*, mass = 97 kg)  
15 385 competitive displacement by the larger *Crocodilus niloticus* (mass = 591 kg) and  
16 386 human colonization have been proposed as possible extinction mechanisms (Brochu,  
17 387 2007). In Australia, human impact is implicated in the extinction of a suite of  
18 388 vertebrates including a small crocodile (*Quinkana fortirostrum*), a giant snake  
19 389 (*Wonambi naracoortensis*) and the huge Megalania (*Varanus priscus*; Prideaux *et al.*,  
20 390 2010; Johnson *et al.*, 2016).

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29 391 Almost all extinct reptiles were island endemics, with insularity highlighted as a key  
30 392 factor increasing a species' extinction risk. Indirect human impact, such as the  
31 393 introduction of invasive carnivores (e.g. *Herpestes auropunctatus*, *Felis catus*) and  
32 394 rats (*Rattus* spp.) is directly linked to the extinction of a wide variety of insular reptile  
33 395 species (e.g. Hedges & Conn, 2012). The introduced Indian mongoose (*Herpestes*  
34 396 *auropunctatus*) had a devastating effect on the Caribbean fauna, being a factor in  
35 397 the extinction of sixteen skink and three snake species (Henderson & Powell, 2009;  
36 398 Hedges & Conn 2012). Interestingly, the only extinct mainland lizard species, the  
37 399 South African *Tetradactylus eastwoodae*, is also the smallest extinct lizard (1.8g).

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46 400 In conclusion, although the current fossil record undoubtedly represents a subset of  
47 401 species that actually went extinct during the Late Quaternary, emergent trends  
48 402 reveal reptile extinction rate was much higher on islands, while a large body  
49 403 represents a further, less straightforward cause for extinction (and only in some  
50 404 reptile groups, but not all). It is clear that relatively recent historical threats were  
51 405 particularly pronounced on insular environments. Some exceptionally large-bodied  
52 406 reptiles were also particularly prone to extinction through human-mediated rapid

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3 407 and prolonged harmful conditions, combined with slow life-histories inhibiting their  
4 408 ability to recover. Recent extinction processes have evidently varied across the  
5 409 reptile phylogeny, geographic area and time, yet body size has often played a role,  
6 410 whether direct or indirect, in the persistence or disappearance of species.  
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11  
12  
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#### 24 418 **SUPPORTING INFORMATION**

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27 419 **Table S1.** Body sizes of extinct reptiles, with references for length-mass conversion  
28 420 equations of lizards, snakes and turtles.  
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31 421 **Table S2.** Body sizes of extant reptiles.  
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#### 34 422 **BIOSKETCH**

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36  
37 423 Alex Slavenko is a PhD student interested in biogeographical patterns of body size  
38 424 and life-history traits and the distribution of species, as well as the general biology of  
39 425 reptiles and amphibians. He is particularly interested in the patterns and evolution of  
40 426 such traits in insular environments.  
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44  
45 427 Oliver Tallowin is a PhD student interested in biogeographical diversity gradients and  
46 428 ecological trends, with a particular focus on how these factors influence reptile and  
47 429 amphibian species extinction risk.  
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883 **TABLES:**

884 **Table 1.** Results of the permutation analyses. For each examined group (e.g., Turtles,  
 885 Caribbean Lizards, Dipsadidae, etc.) are listed the means and sample sizes of the  
 886 examined groups, as well as the corresponding p-values. The larger value of each  
 887 two compared means and significant p-values (with  $\alpha = 0.05$ ) are in bold. p-values of  
 888 0 mean that none of the 100,000 iterations had a t-statistic as extreme as the  
 889 observed.

	Extinct		Extant		p-value
	Mean	n	Mean	n	
Reptiles	<b>867 g</b>	82	22.5 g	10090	<b>0</b>
Lizards	<b>88.9 g</b>	45	9.5 g	6045	<b>0</b>
Lizards (no fossils)	<b>38.6 g</b>	29	9.5 g	6045	<b>0.0002</b>
Snakes	<b>126.9 g</b>	9	61.7 g	3513	0.51
Turtles	<b>61.6 kg</b>	24	3.8 kg	318	<b>0</b>
Crocodiles	68 kg	4	<b>191.9 kg</b>	24	<b>0.04</b>
Caribbean Lizards	<b>43.3 g</b>	31	6.8 g	377	<b>0</b>
Mascarene Lizards	<b>15.2 g</b>	5	7.3 g	19	0.19
Galapagos Tortoises	113.5 kg	3	<b>134.9 kg</b>	7	0.29
Size-bias in the fossil record of extant species					
	Fossils		All		p-value
	Mean	n	Mean	n	
Reptiles	<b>350.6 g</b>	261	22.5 g	10090	<b>0</b>
Lizards	<b>69.5 g</b>	94	9.5 g	6045	<b>0</b>
Snakes	<b>297.7 g</b>	105	61.7 g	3513	<b>0</b>
Turtles	<b>4.2 kg</b>	48	3.8 kg	318	0.72
Crocodiles	<b>228.3 kg</b>	9	191.9 kg	24	0.6
Geographically weighted analyses					
	Extinct		Extinct		p-value
	Mean	n	Mean	n	
Reptiles	<b>867 g</b>	82	22.5 g	10090	<b>0</b>



Lizards	<b>88.9 g</b>	45	9.5 g	6045	<b>0</b>
Lizards (no fossils)	<b>38.6 g</b>	29	9.5 g	6045	<b>0.0006</b>
Snakes	<b>126.9 g</b>	9	61.7 g	3513	0.54
Turtles	<b>61.6 kg</b>	24	3.8 kg	318	<b>0</b>
Insular Endemics Only					
	Extinct		Extant		p-value
	Mean	n	Mean	n	
Reptiles	<b>589.3 g</b>	73	14.5 g	2627	<b>0</b>
Lizards	<b>80.7 g</b>	43	8.4 g	1832	<b>0</b>
Snakes	<b>56.6 g</b>	8	40.9 g	741	0.68
Turtles	<b>68.7 kg</b>	19	8.6 kg	34	<b>0</b>
Crocodyles	59 kg	3	<b>166 kg</b>	3	<b>0.05</b>
Extant Only					
	Insular Endemic		Mainland		p-value
	Mean	n	Mean	n	
Reptiles	14.5 g	2627	<b>26.2 g</b>	7463	<b>0</b>
Lizards	8.4 g	1832	<b>10 g</b>	4213	<b>0</b>
Snakes	40.9 g	741	<b>68.8 g</b>	2782	<b>0.001</b>
Turtles	<b>8.6 kg</b>	34	3.1 kg	284	<b>0.01</b>
Crocodyles	166 kg	3	<b>195.9 kg</b>	21	0.67
Families					
	Extinct		Extant		p-value
	Mean	n	Mean	n	
Dipsadidae	<b>153.6 g</b>	4	39 g	745	<b>0.02</b>
Gekkonidae	<b>20.1 g</b>	3	4.8 g	1034	0.37
Iguanidae	<b>3 kg</b>	3	1.6 kg	41	0.21
Lacertidae	<b>3.8 kg</b>	2	8.5 g	319	0.08
Leiocephalidae	<b>61.3 g</b>	9	18.3 g	20	<b>0.05</b>
Scincidae	<b>32.6 g</b>	20	6 g	1559	<b>0.0003</b>
Teiidae	<b>160.2 g</b>	2	44.2 g	148	0.22
Testudinidae	<b>60 kg</b>	20	7.9 kg	51	<b>0</b>

	Genera				
	Extinct		Extant		p-value
	Mean	n	Mean	n	
<i>Alinea</i>	<b>22.3 g</b>	2	18.5 g	2	0.83
<i>Ameiva</i>	<b>160.2 g</b>	2	63.7 g	30	0.24
<i>Chelonoidis</i>	48.8 kg	10	<b>98.6 kg</b>	11	0.12
<i>Hypsirhynchus</i>	<b>130.8 g</b>	2	72 g	7	0.44
<i>Leiocephalus</i>	<b>61.3 g</b>	9	18.3 g	20	<b>0.05</b>
<i>Leiopisma</i>	<b>383.2 g</b>	2	25.5 g	2	0.33
<i>Mabuya</i>	<b>23.4 g</b>	5	20.9 g	3	0.63
<i>Phelsuma</i>	<b>62.2 g</b>	2	4.5 g	50	0.19
<i>Spondylurus</i>	11.9 g	4	<b>13.3 g</b>	13	0.79

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Peer Review

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3 892 **FIGURE LEGENDS:**  
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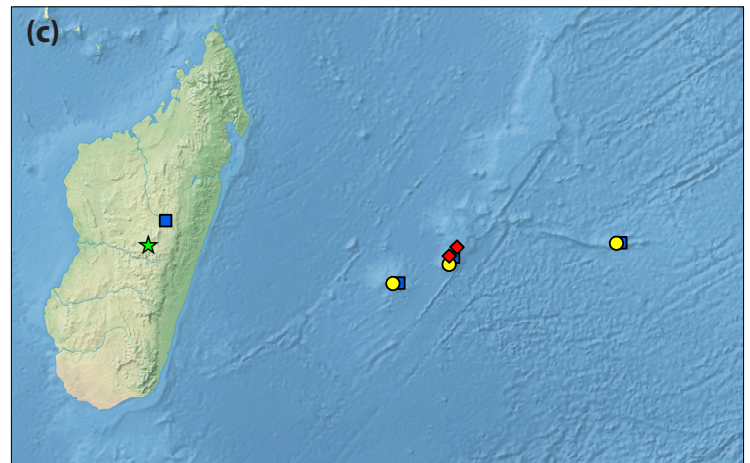
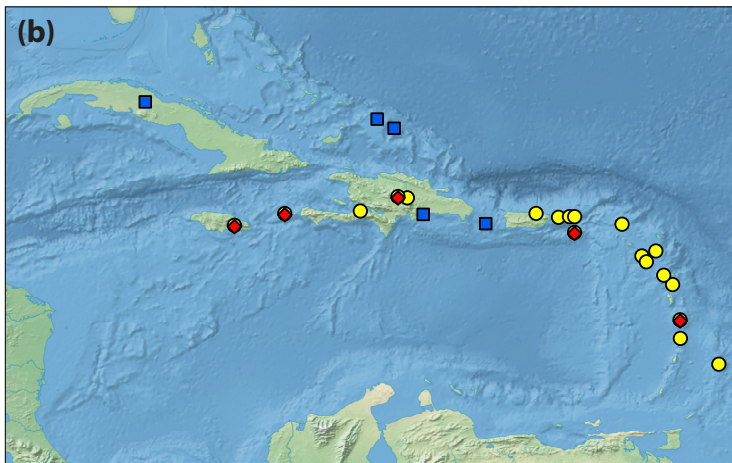
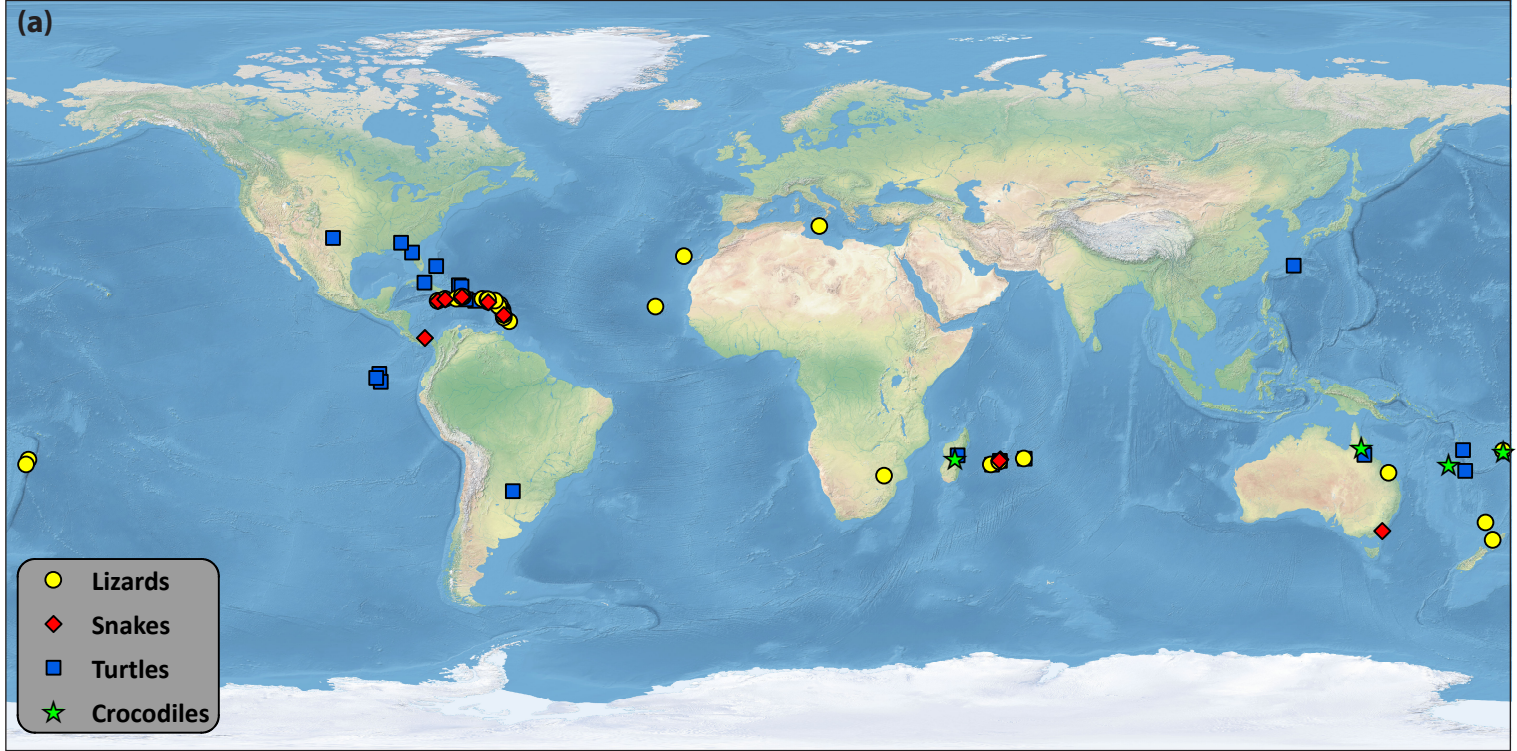
5 893 **Figure 1.** (a) Map showing the distribution of extinct reptile species, where yellow  
6 894 circles represent lizards, red diamonds represent snakes, blue squares represent  
7 895 turtles, and green stars represent crocodiles. Also presented are close-ups of the  
8 896 map in (b) the Caribbean and (c) the Mascarenes and Madagascar.

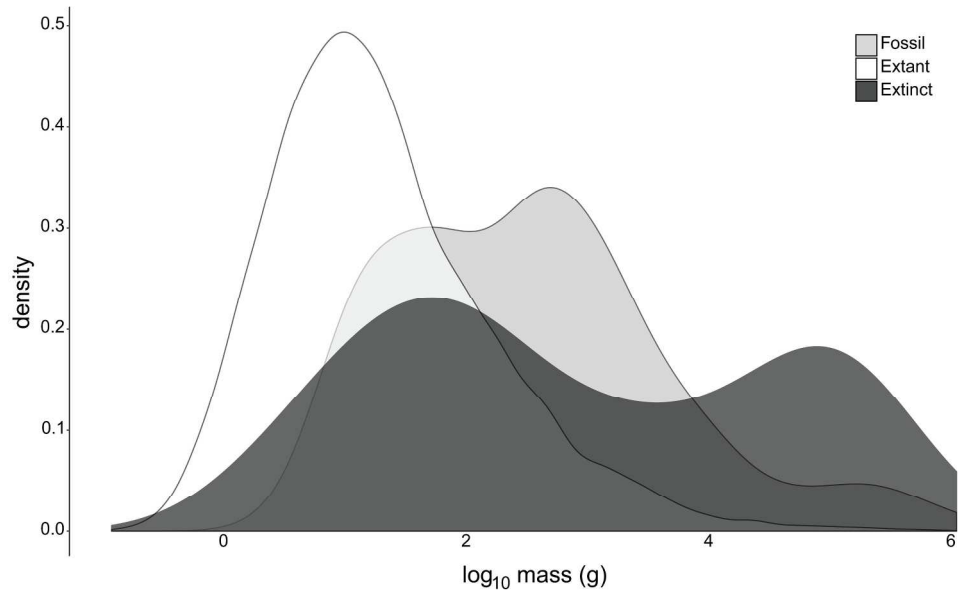
9 897 **Figure 2.** Density plot of reptile body sizes, with extant species in white, extant  
10 898 species represented in the fossil record in light grey, and extinct species in dark grey.  
11 899 The two peaks in extinct species body sizes correspond to the smaller-sized  
12 900 squamates (lizards and snakes) and to the larger-bodied turtles and crocodiles.

13 901 **Figure 3.** Body size distributions of extant (white) and extinct (black) species of (a)  
14 902 lizards, (b) snakes, (c) turtles and (d) crocodiles. Mean body sizes of each group are  
15 903 represented by triangles.

16 904 **Figure 4.** Plots showing the ratio between insular endemics (black) and mainland  
17 905 species (white) are presented for (a) lizards, (b) snakes, (c) turtles, and (d) crocodiles.  
18 906 The dashed red line represents, in each taxon, the predicted ratio between insular  
19 907 endemics and mainland species for both extinct and extant species under a null  
20 908 hypothesis of equal extinction frequencies on islands and mainlands.

21 909 **Figure 5.** Body sizes of extant and extinct species of reptiles in each (a) family and (b)  
22 910 genus examined. Body sizes were compared using permutation tests: \* $p < 0.05$ ; \*\* $p$   
23 911  $< 0.01$ ; \*\*\* $p < 0.001$ .  
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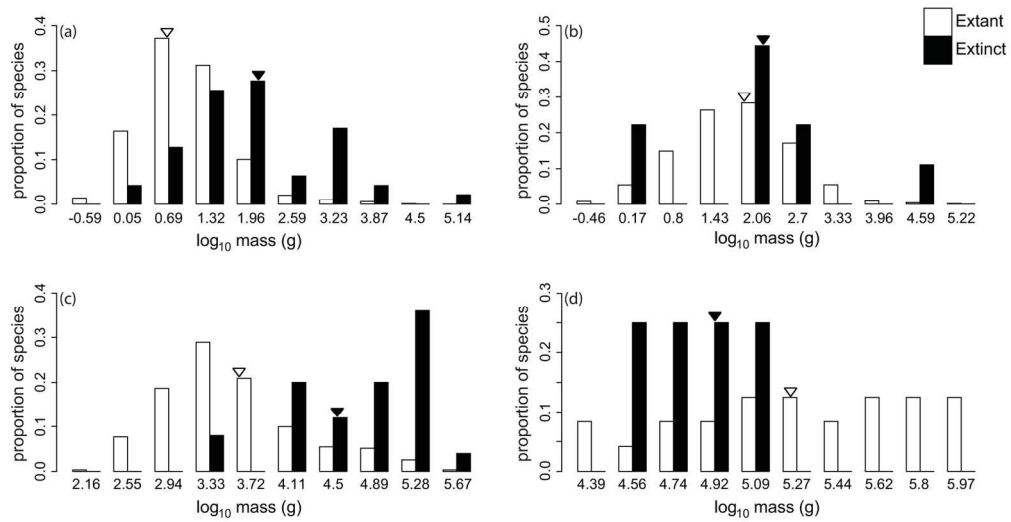


**Figure 2.** Density plot of reptile body sizes, with extant species in white, extant species represented in the fossil record in light grey, and extinct species in dark grey. The two peaks in extinct species body sizes correspond to the smaller-sized squamates (lizards and snakes) and to the larger-bodied turtles and crocodiles.

216x128mm (300 x 300 DPI)

Review

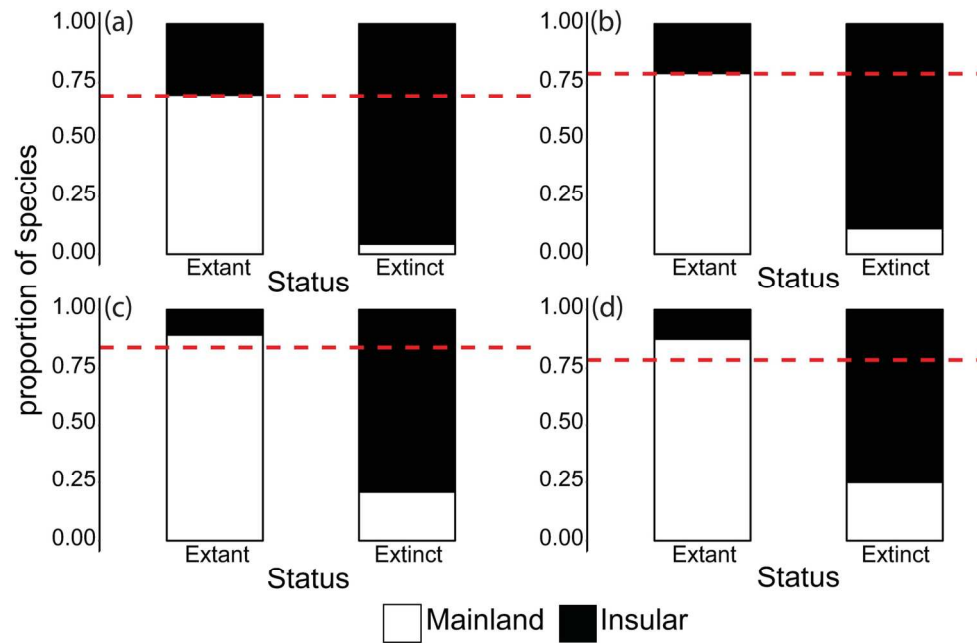




**Figure 3.** Body size distributions of extant (white) and extinct (black) species of (a) lizards, (b) snakes, (c) turtles and (d) crocodiles. Mean body sizes of each group are represented by triangles.  
156x83mm (300 x 300 DPI)

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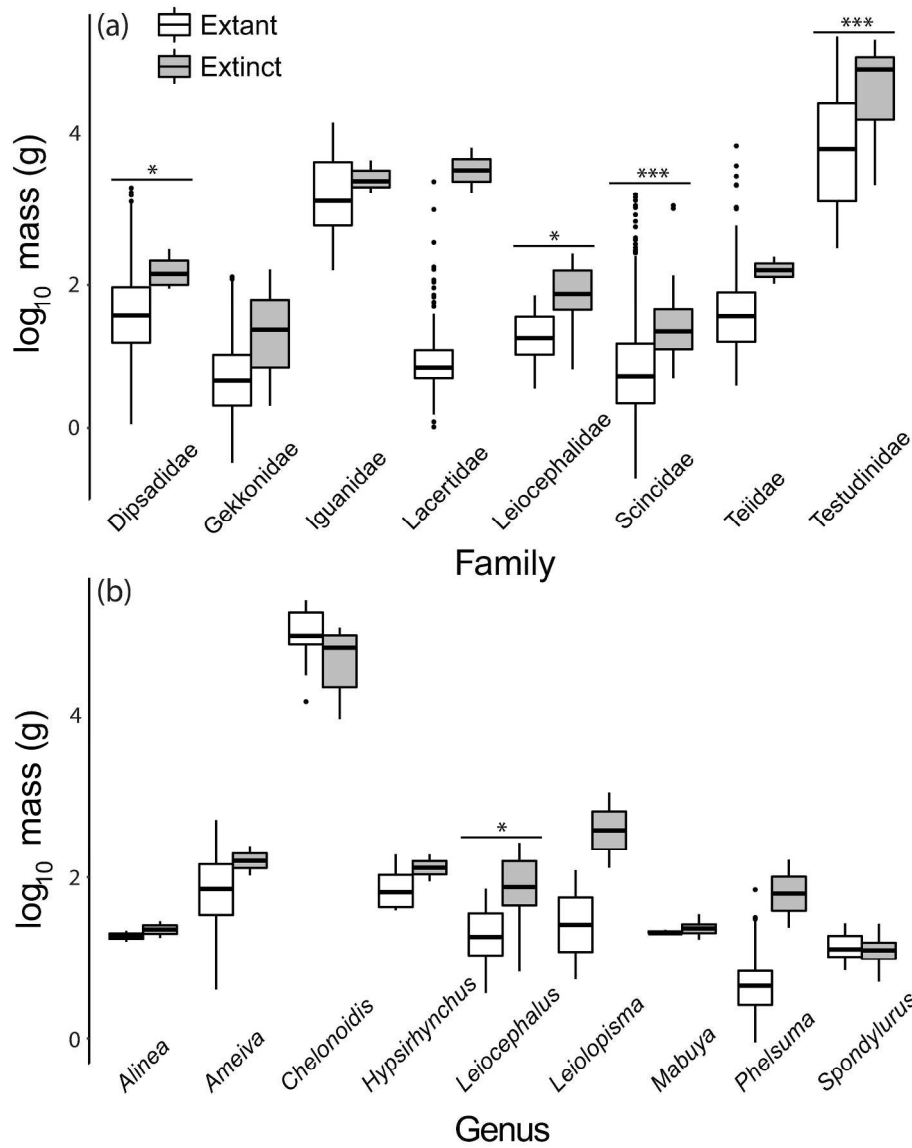
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**Figure 4.** Plots showing the ratio between insular endemics (black) and mainland species (white) are presented for (a) lizards, (b) snakes, (c) turtles, and (d) crocodiles. The dashed red line represents, in each taxon, the predicted ratio between insular endemics and mainland species for both extinct and extant species under a null hypothesis of equal extinction frequencies on islands and mainlands.

143x94mm (300 x 300 DPI)





**Figure 5.** Body sizes of extant and extinct species of reptiles in each (a) family and (b) genus examined. Body sizes were compared using permutation tests: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .  
217x285mm (300 x 300 DPI)