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64 **Abstract**

65 The distributions of amphibians, birds and mammals have underpinned global and local
66 conservation priorities, and have been fundamental to our understanding of the determinants of
67 global biodiversity. In contrast, the global distributions of reptiles, representing a third of
68 terrestrial vertebrate diversity, have been unavailable. This prevented reptiles' incorporation into
69 conservation planning and biased our understanding of the underlying processes governing
70 global vertebrate biodiversity. Here, we present and analyse the global distribution of 10,064
71 reptile species (99% of extant terrestrial species). We show that richness patterns of the other
72 three tetrapod classes are good spatial surrogates for species richness of all reptiles combined and
73 of snakes, but characterize diversity patterns of lizards and turtles poorly. Hotspots of total and
74 endemic lizard richness overlap very little with those of other taxa. Moreover, existing protected
75 areas, sites of biodiversity significance and global conservation schemes, represent birds and
76 mammals better than reptiles. We show that additional conservation actions are needed to
77 effectively protect reptiles, particularly lizards and turtles. Adding reptile knowledge to a global
78 complementarity conservation priority scheme, identifies many locations that consequently
79 become important. Notably, investing resources in some of the world's arid, grassland, and
80 savannah habitats might be necessary to represent all terrestrial vertebrates efficiently.

81 **Introduction**

82 Our knowledge of the distributions of a broad variety of organisms has improved greatly in the
83 past decade¹⁻³. This has greatly aided our efforts to conserve biodiversity⁴⁻⁶ and significantly
84 enhanced our grasp of broad scale evolutionary and ecological processes⁷⁻¹². Nevertheless,
85 despite comprising one third of terrestrial vertebrate species, knowledge of reptile distributions
86 remained poor and unsystematic. This represented a major gap in our understanding of the
87 global structure of biodiversity and our ability to conserve nature. Historically, broad-scale
88 efforts towards the protection of land vertebrates (and thus also of reptiles) have been based
89 predominantly on data from plants, birds, mammals and to a lesser degree amphibians¹³⁻¹⁵. Here
90 we present complete species-level global distributions of nearly all reptiles: 10,064 known,
91 extant, terrestrial species for which we could identify precise distribution information. These
92 distributions cover the Sauria (lizards, 6110 species), Serpentes (snakes, 3414 species),
93 Testudines (turtles, 322 species), Amphisbaenia ('worm lizards', 193 species), Crocodylia
94 (crocodiles, 24 species) and Rhynchocephalia (the tuatara, one species).

95 This dataset completes the global distribution mapping of all described, extant, terrestrial
96 vertebrates (Fig. 1a), providing information that has been missing from much of the global
97 conservation planning and prioritization schemes constructed over the last twenty years⁴. We use
98 our reptile distribution data to: a) examine the congruence in general, hotspot, and endemism
99 richness patterns across all tetrapod classes and among reptile groups; b) explore how current
100 conservation networks and priorities represent reptiles; and c) suggest regions in need of
101 additional conservation attention to target full terrestrial vertebrate representation and highlight
102 current surrogacy gaps, using a formal conservation prioritisation technique.

104 **Results and Discussion**

105 ***Species richness of reptiles compared to other tetrapods***

106 The global pattern of reptile species richness (Fig. 1b) is largely congruent with that of all other
107 terrestrial vertebrates combined ($r = 0.824$, e.d.f. = 31.2, $p \ll 0.0001$; Figs. 2a, S1, Table S1).
108 However, the major reptile groups (Figs. 1c-e, 2b-c, S1, Table S1) show differing degrees of
109 congruence with the other tetrapod taxa. The richness distribution of snakes (Fig. 1d) is very
110 similar to that of other tetrapods (Fig. 2c) in showing pan-tropical dominance ($r = 0.873$, e.d.f. =
111 30.2, $p \ll 0.0001$). Lizard richness is much less similar to non-reptilian tetrapod richness ($r =$
112 0.501 , e.d.f. = 38.3, $p \ll 0.001$, Fig. 2b). It is high in both tropical and arid regions, and notably
113 in Australia (Figs. 1c, S1). Turtle richness is also less congruent with diversity patterns of the
114 other tetrapods ($r = 0.673$, e.d.f. = 55.2, $p \ll 0.001$), and peaks in the south-eastern USA, the
115 Ganges Delta, and Southeast Asia (Fig. 1e).

116 Snakes dominate reptile richness patterns due to their much larger range sizes compared to
117 lizards, even though lizards are about twice as speciose (median ranges size for 3414 snake
118 species: 62,646 km²; for 6415 lizard species: 11,502 km²; Fig. S2). Therefore snakes,
119 disproportionally influence global reptile richness patterns^{16,17} (Table S1, Fig. S1).

120 ***Hotspots of richness and range-restricted species***

121 As with overall richness patterns, hotspots of richness (the richest 2.5%, 5%, 7.5% and 10% of
122 grid-cells) for all reptiles combined, and of snakes, are largely congruent with those of other
123 tetrapod classes. However they are incongruent with hotspots of lizard or turtle richness (Figs. 3;
124 S3).

125 Congruence in the richness of range-restricted species (those species with the smallest 25% or
126 10% ranges in each group) between tetrapod groups is lower than the congruence across all
127 species¹ (Table S1). Endemic lizard and turtle distributions are least congruent with the endemics
128 in other tetrapod classes (Table S1). Global hotspots of relative endemism (or range-size
129 weighted richness, see Methods) for reptiles differ from those of non-reptilian tetrapods (Fig.
130 S4). Island faunas in places such as Socotra, New Caledonia and the Antilles are highlighted for
131 reptiles, while hotspots of endemism for non-reptilian tetrapods are more often continental.

132 *The utility of protected areas and current priority schemes in capturing reptile richness*

133 Reptiles, like amphibians, are poorly represented in the global network of protected areas (Table
134 S2; Figs. S5, S6). Only 3.5% of reptile and 3.4% of amphibian species distributions are
135 contained in protected areas (median species range overlap per class, with IUCN categories I-
136 IV), compared with 6.5% for birds and 6% for mammals. Within reptile groups, strict protected
137 areas (IUCN Category I) overlap less with lizard ranges than with other reptile groups but there
138 are no important differences between taxa for the more permissive protected area types (Table
139 S2; Fig. S5). Amphibians have the highest proportion of species whose ranges lie completely
140 outside protected areas, when compared to the other tetrapod groups. Lizards, also fare poorly
141 and have the highest proportion of species outside protected areas when compared to the other
142 reptile groups (Fig. S6a). Turtles have the lowest proportion of species with at least 10% of their
143 range covered by protected areas (Fig. S6b). We suggest that these low overlaps may have been
144 caused by the inability to consider reptile diversity for direct protection, probably arising from
145 ignorance of their distributions.

146 We explored the coverage of all tetrapods in three global prioritisation schemes^{13,14,18} and a
147 global designation of sites for biodiversity significance¹⁵ that have recently used distribution data

148 to highlight regions for targeted conservation. These four global prioritisations/designations
149 cover 6.8%-37.4% of the Earth's land surface with 34-11,815 unique sites. Terrestrial vertebrate
150 groups have 68%-98% of their species with at least some range covered by these schemes (Fig.
151 S6c). However, reptiles and amphibians are sampled least well by these global schemes, and
152 within reptiles lizards have the lowest representation (Fig. S6c).

153 Fortunately, reptiles seem better situated in terms of conservation costs compared to other
154 tetrapods. The median conservation opportunity cost¹⁹ (using the loss of agricultural revenue as a
155 proxy for land-cost) for reptiles is lower than that for other tetrapods ($F_{3, 31850} = 17.4$, $p < 0.001$;
156 Fig. S7). Within reptiles, the opportunity cost is lowest for lizards, and highest for turtles and
157 crocodiles, which could reflect their greater dependence on fresh-water habitats ($F_{3, 10060} = 88.4$,
158 $p < 0.001$; Fig. S7b).

159 *Conservation priorities for all tetrapods, incorporating reptile distributions*

160 Our results suggest that reptiles, and particularly lizards and turtles, need to be better
161 incorporated into conservation schemes. We used relative endemism within a complementarity
162 analysis²⁰ to identify broad areas within which international and local conservation action should
163 reduce reptile extinction risk (Figs. 4, S8), and repeated this analysis to also incorporate
164 conservation opportunity costs¹⁹ (Fig. S8d,e). Many previously identified priority regions^{13,14},
165 have been retained with the addition of reptile distributions. These include northern and western
166 Australia; central southern USA and the gulf coast of Mexico; the Brazilian Cerrado; Southeast
167 Asia, and many islands.

168 Nevertheless, our analyses also reveal many regions, not currently perceived as biodiversity
169 conservation priorities for tetrapods. These priority areas are predominantly arid and semi-arid

170 habitats (see also Fig. S8f for mean rank change per biome, for prioritisation with and without
171 reptiles). They include parts of northern Africa through the Arabian Peninsula and the Levant;
172 around Lake Chad; in inland arid southern Africa; central Asian arid highlands and steppes;
173 central Australia; the Brazilian Caatinga, and the southern Andes. These regions have been
174 previously neglected as their non-reptile vertebrate biotas were more efficiently represented in
175 other locations. Our analyses show that those locations were poor spatial surrogates for reptile
176 distributions and that conservation efforts in our suggested locations may afford better protection
177 for reptiles while maintaining efficient representation of other vertebrates. We note that many of
178 these locations have low conservation opportunity costs so may be especially attractive for
179 conservation. Furthermore, the location of these areas is not primarily driven by conservation
180 opportunity costs. When these costs are incorporated into the analyses, very similar regions are
181 highlighted for special attention due to the inclusion of reptile distributions (Fig. S8d,e).

182 *Summation*

183 The complete map of tetrapod species richness presented here reveals important and unique
184 properties of reptile diversity, particularly of lizards and turtles (Figs. 1-3). At a regional scale
185 reptiles have previously been shown to be unusually diverse in arid and semi-arid habitats²¹⁻²³.
186 Here we reveal that this pattern is global, and further show reptile prominence in island faunas
187 (Figs. 2d, S4). Furthermore, we show that reptiles' unique diversity patterns have important
188 implications for their conservation. Targeted reptile conservation lags behind that of other
189 tetrapod classes, probably through ignorance²⁴⁻²⁶. The distributions provided here could make a
190 vital contribution to bridging this gap. Concentrations of rare species in unexpected locations
191 (Fig. 4) require explicit consideration when planning conservation actions. Highlighting such
192 locations for new taxa could be especially beneficial for resource-constrained planning,

193 especially where land costs are low. The lower global congruence with recognized diversity
194 patterns for reptiles should also serve as a warning sign, contrary to some recent suggestions²⁷,
195 for our ability to use distributions of well-studied groups in order to predict diversity patterns of
196 poorly known taxa. The distinctive distribution of reptiles, and especially of lizards, suggests that
197 it is driven by different ecological and evolutionary processes to those in other vertebrate
198 taxa^{23,28}. The complete distributions of terrestrial tetrapods we now possess could greatly
199 enhance our ability to study, understand and protect nature.

200

201 **Methods**

202 Data collection and assembly was carried out by members of the Global Assessment of Reptile
203 Distributions (GARD) group, which includes all the authors of this paper. Regional specialist
204 group members supervised the integration of geographic data for all species from field guides
205 and books covering the terrestrial reptilian fauna of various regions, as well as revised museum
206 specimen databases, online meta-databases (including the IUCN, GBIF and Vertnet), our own
207 observations and the primary literature. We followed the taxonomy of the March 2015 edition of
208 the Reptile Database²⁹. Source maps were split or joined on that basis. We used the newest
209 sources available to us. Polygonal maps - representing species extent of occurrence - were
210 preferred over other map types, as such distribution representations are those available for the
211 other classes that were compared to reptiles. Point locality data were modelled to create polygons
212 representing the extent of occurrence using hull geometries (see supplement). Gaps in reptile
213 distribution knowledge for particular locations or taxa were filled using *de novo* polygon and
214 gridded maps created by GARD members specializing in the fauna of particular regions and
215 taxa. These maps and all data obtained from online databases and the primary literature were

216 then internally vetted, in a manner analogous to the IUCN Specialist Group process. Further
217 details on data collection and curation, modelling of point localities and a full list of data sources
218 per species are available in the supplement. Overall we analysed distribution maps for 10,064
219 extant species, which represent 99% of the species found in the Reptile Database of March 2015.
220 For all analytical purposes we contrasted snakes with the paraphyletic 'lizards' (here defined as
221 lepidosaurs exclusive of snakes).

222 Polygonal representations of the extent of species' occurrences, such as we assembled and use in
223 our analyses, are fundamentally important to contemporary conservation planning³⁰. The IUCN's
224 assessment of the extinction risk of individual species requires (and produces) such data, and
225 both they and many other organisations and researchers have used such data in aggregate and at
226 regional-to-global scales for several decades³¹. Like any representation of species distributions,
227 polygonal range maps can include errors both of omission and commission. Both kinds of
228 inaccuracy can lead to erroneous conclusions by unwary users and this has led to some
229 controversy over the use of polygonal range maps. Of course, all biogeographic representations -
230 specimen localities, SDM outputs, atlas data, polygonal maps and explorers' narratives - lie along
231 this omission: commission spectrum, and can equally be misused or found useless³². For global
232 prioritisation, we follow a comprehensive recent study³³ demonstrating the effectiveness of
233 polygonal range maps in highlighting priority areas, despite errors at the level of individual
234 species. We do, however, recognise that specimen data, if collected, curated and made available
235 (at a suitable scale) remains a gold standard for some uses³⁴.

236 Our grid-cell analyses were conducted in a Behrmann Equal Area projection of 48.25 km grid-
237 cells ($\sim 0.5^\circ$ at 30°N/S). All analyses were repeated at a grid size of 96.5 km ($\sim 1^\circ$ at 30°N/S) and

238 results were qualitatively unchanged. GIS and statistical analyses were carried out in R and
239 PostGIS.

240 Range size weighted richness (rswr) was calculated, for each cell, using the following formula:

241 $rswr_i = \sum_j q_{ij}$ where q_{ij} is the fraction of the distribution of the species j in the cell i .

242 We used ‘Zonation’²⁰ to produce a ranked prioritisation amongst cells, assuming equal weight to
243 all species and assuming an equal cost for all cells. Cell value was the maximum proportion of
244 any species range represented in it. Cell priority was calculated by iteratively removing the least
245 valuable cell and updating cell values²⁰. We analysed all tetrapod species combined and
246 tetrapods without reptiles separately, to reveal the change in rank importance induced by adding
247 reptile distributions (See supplement, Fig. S8). We repeated our prioritisation using per-cell
248 agricultural opportunity costs¹⁹, and found via rank correlation that our priority regions are fairly
249 insensitive to the use of land costs (Figs. 4, S8).

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265 **Author contributions**

266 AMB, RG, SM, UR conceived the study. RG, CDLO, UR designed the analyses. UR conducted
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270 PW, YW provided, collated, and verified underlying data. All authors read and commented on
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272 UR, AF and MN contributed equally to the paper. RG and SM contributed equally to the paper.

273 **Competing interests**

274 All authors declare no competing interests.

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278 **Data availability**

279 The reptile distribution data used in this study are available from Dryad (doi TBA)

280

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363 **Figure captions**

364 Figure 1 – Species richness maps of terrestrial tetrapods a) Richness of all tetrapods (reptiles,
365 amphibians, birds and mammals). b-e: species richness of reptile groups b) all reptiles, c)
366 ‘lizards’ d) snakes, e) turtles. Grey areas denote terrestrial regions devoid of species in a
367 particular group. Blue colours denote regions with few species and red ones denote regions with
368 many species (note that the scale differs between panels). All maps in an equal area, Behrman
369 projection at a 48.25 *48.25 km grid-cell resolution).

370 Figure 2 – Comparing reptile richness to other tetrapods. Hexagon scatter plots comparing
371 species richness values per grid-cell with binning (black line indicates a loess fit, $\alpha=0.6$) of
372 tetrapods without reptiles, to a) all reptiles, b) ‘lizards’ and c) snakes. d) a map of the ratio of
373 reptile richness to non-reptilian tetrapod richness per grid cell (note the wide range of values for
374 the top category). Hatched regions designate areas where this proportion in the top 5% (black)
375 and 25% (grey).

376 Figure 3 –Species richness hotspots of reptiles and reptile groups. In each panel the lightest
377 colour denote the 10% of 48.25*48.25 km grid-cells with the highest numbers of species, and as
378 the colours get darker they represent the top 7.5%, 5% and richest 2.5% cells respectively. a) all
379 reptiles, b) lizards, c) snakes, and d) turtles.

380 Figure 4 – Key areas for tetrapod conservation, highlighting regions that rise in importance for
381 conservation due to inclusion of reptiles. Cells were ranked in a formal prioritisation scheme²⁰,
382 based on complementarity when ranking cells in an iterative manner. Cells were ranked twice, I-
383 with all tetrapods, II- with all tetrapods excluding reptiles. a) Patterns per 0.5 degree grid-cell
384 where colours represent the priority ranks for the scheme which included all tetrapods (blue =

385 low, red = high). The cells that are highlighted with the bold foreground colours are those that
386 pinpoint those regions that gain in conservation importance due to the inclusion of the reptile
387 data. These cells were selected following these two rules (i) they were in the top 10% of increase
388 in rank, when subtracting the ranks of the analysis with reptiles from the ranks of the analysis
389 without them; and (ii) were part of statistically significant spatial clusters of rank changes (using
390 local Moran's I^{35}). b) The mean change in rank between prioritizations with and without reptiles
391 (using the above method), per ecoregion (red- ecoregions that become more important due to the
392 inclusion of reptile information; blue – ecoregions becoming less important).