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61 **Summary**

62 The distributions of amphibians, birds and mammals¹⁻³ have underpinned global and local
63 conservation priorities⁴⁻⁶, and have been fundamental to our understanding of the determinants of
64 global biodiversity^{7,8}. In contrast, the global distributions of reptiles, representing a third of
65 terrestrial vertebrate diversity, have been unavailable. This prevented reptiles' incorporation into
66 conservation planning and biased our understanding of the underlying processes governing
67 global vertebrate biodiversity. Here, we present and analyse, for the first time, the global
68 distribution of 10,064 reptile species (99% of extant terrestrial species). We show that richness
69 patterns of the other three tetrapod classes are good spatial surrogates for species richness of all
70 reptiles combined and of snakes, but characterize diversity patterns of lizards and turtles poorly.
71 Hotspots of total and endemic lizard richness overlap very little with those of other taxa.
72 Moreover, existing protected areas, sites of biodiversity significance and global conservation
73 schemes, represent birds and mammals better than reptiles. We show that additional conservation
74 actions are needed to effectively protect reptiles, particularly lizards and turtles. Adding reptile
75 knowledge to a global complementarity conservation priority scheme, identifies many new
76 locations that consequently become important. Notably, investing resources in some of the
77 world's arid, grassland, and savannah habitats will be necessary to represent all terrestrial
78 vertebrates efficiently.

79 **Introduction**

80 Our knowledge of the distributions of a broad variety of organisms has improved greatly in
81 recent years, and significantly enhanced our grasp of broad scale evolutionary and ecological
82 processes⁹⁻¹². Nevertheless, despite comprising one third of terrestrial vertebrate species,
83 knowledge of reptile distributions remained poor and unsystematic. This represented a major gap
84 in our understanding of the global structure of biodiversity and our ability to conserve nature.
85 Historically, broad-scale efforts towards the protection of land vertebrates (and thus also of
86 reptiles) have been based predominantly on data from plants, birds, mammals and to a lesser
87 degree amphibians¹³⁻¹⁵. Here we present complete species-level global distributions of nearly all
88 reptiles: 10,064 known, extant, terrestrial species for which we could identify precise distribution
89 information. These distributions cover the Sauria (lizards, 6110 species), Serpentes (snakes, 3414
90 species), Testudines (turtles, 322 species), Amphisbaenia ('worm lizards', 193 species),
91 Crocodylia (crocodiles, 24 species) and Rhynchocephalia (the tuatara, one species).

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

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

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

113 Snakes dominate reptile richness patterns due to their much larger range sizes compared to
114 lizards, even though lizards are about twice as speciose (median ranges size for 3414 snake
115 species: 62,646 km²; for 6415 lizard species: 11,502 km²; Extended Data Fig. 2). Therefore
116 snakes, disproportionally influence global reptile richness patterns^{16,17} (Extended Data Table 1,
117 Extended Data Fig. 1).

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

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

123 Congruence in the richness of range-restricted species (those species with the smallest 25% or
124 10% ranges in each group) between tetrapod groups is lower than the congruence across all
125 species¹ (Extended Data Table 1). Endemic lizard and turtle distributions are least congruent
126 with the endemics in other tetrapod classes (Extended Data Table 1). Global hotspots of relative
127 endemism (or range-size weighted richness, see Methods) for reptiles differ from those of non-
128 reptilian tetrapods (Extended Data Fig. 4). Island faunas in places such as Socotra, New
129 Caledonia and the Antilles are highlighted for reptiles, while hotspots of endemism for non-
130 reptilian tetrapods are more often continental.

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

132 Reptiles, like amphibians, are poorly represented in the global network of protected areas
133 (Extended Data Tables 1; Extended Data Figs. 5-6). Only 3.5% of reptile and 3.4% of amphibian
134 species distributions are contained in protected areas (median species range overlap per class,
135 with IUCN categories I-IV), compared with 6.5% for birds and 6% for mammals. Within reptile
136 groups, strict protected areas (IUCN Category I) overlap less with lizard ranges than with other
137 reptile groups but there are no important differences between taxa for the more permissive
138 protected area types (Extended Data Tables 2; Extended Data Fig. 5). Amphibians have the
139 highest proportion of species whose ranges lie completely outside protected areas, when
140 compared to the other tetrapod groups. Lizards, also fare poorly and have the highest proportion
141 of species outside protected areas when compared to the other reptile groups (Extended data Fig.
142 6a). Turtles have the lowest proportion of species with at least 10% of their range covered by
143 protected areas (Extended data Fig. 6b). 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
151 (Extended data Fig. 6c). However, reptiles and amphibians are sampled least well by these global
152 schemes, and within reptiles lizards have the lowest representation (Extended Data Fig. 6c).

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 Extended Data Fig. 7). Within reptiles, the opportunity cost is lowest for lizards, and highest for
157 turtles and crocodiles, which could reflect their greater dependence on fresh-water habitats ($F_{3,$
158 $10060} = 88.4$, $p < 0.001$; Extended Data Fig. 7b).

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 (Fig. 4), and repeated this analysis to also incorporate conservation
164 opportunity costs¹⁹ (Extended Data Fig. 8d,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 new regions, not currently perceived as biodiversity
169 conservation priorities for tetrapods. These new priority areas are predominantly arid and semi-
170 arid habitats (see also Extended Data Fig. 8f for mean rank change per biome, for prioritisation
171 with and without reptiles). They include parts of northern Africa through the Arabian Peninsula
172 and the Levant; around Lake Chad; in inland arid southern Africa; central Asian arid highlands
173 and steppes; central Australia; the Brazilian Caatinga, and the southern Andes. These regions
174 have been previously neglected as their non-reptile vertebrate biotas were more efficiently
175 represented in other locations. Our analyses show that those locations were poor spatial
176 surrogates for reptile distributions and that conservation efforts in our new suggested locations
177 may afford better protection for reptiles while maintaining efficient representation of other
178 vertebrates. We note that many of these novel locations have low conservation opportunity costs
179 so may be especially attractive for conservation. Furthermore, the location of these areas is not
180 primarily driven by conservation opportunity costs. When these costs are incorporated into the
181 analyses, very similar regions are highlighted for special attention due to the inclusion of reptile
182 distributions (Extended Data Fig. 8d,e).

183 **Discussion**

184 The complete map of tetrapod species richness presented here reveals important and unique
185 properties of reptile diversity, particularly of lizards and turtles (Figs. 1-3). At a regional scale
186 reptiles have previously been shown to be unusually diverse in arid and semi-arid habitats²¹⁻²³.
187 Here we reveal that this pattern is global, and further show reptile prominence in island faunas
188 (Fig. 2d, Extended Data Fig. 4). Furthermore, we show that reptiles' unique diversity patterns
189 have important implications for their conservation. Targeted reptile conservation lags behind that
190 of other tetrapod classes, probably through ignorance²⁴⁻²⁶. The distributions provided here could

191 make a vital contribution to bridging this gap. Concentrations of rare species in unexpected
192 locations (Fig. 4) require explicit consideration when planning conservation actions.
193 Highlighting such locations for new taxa could be especially beneficial for resource-constrained
194 planning, especially where land costs are low. The lower global congruence with recognized
195 diversity patterns for reptiles should also serve as a warning sign, contrary to some recent
196 suggestions²⁷, for our ability to use distributions of well-studied groups in order to predict
197 diversity patterns of poorly known taxa. The distinctive distribution of reptiles, and especially of
198 lizards, suggests that it is driven by different ecological and evolutionary processes to those in
199 other vertebrate taxa^{23,28}. The complete distributions of terrestrial tetrapods we now possess
200 could greatly enhance our ability to study, understand and protect nature.

201

202 **Methods**

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

214 distribution knowledge for particular locations or taxa were filled using *de novo* polygon and
215 gridded maps created by GARD members specializing in the fauna of particular regions and
216 taxa. These maps and all data obtained from online databases and the primary literature were
217 then internally vetted, in a manner analogous to the IUCN Specialist Group process. Further
218 details on data collection and curation, modelling of point localities and a full list of data sources
219 per species are available in the supplement. Overall we analysed distribution maps for 10,064
220 extant species, which represent 99% of the species found in the Reptile Database of March 2015.
221 For all analytical purposes we contrasted snakes with the paraphyletic ‘lizards’ (here defined as
222 lepidosaurs exclusive of snakes).

223 Analyses were conducted in a Behrmann Equal Area projection of 48.25 km grid-cells (~0.5° at
224 30°N/S). All analyses were repeated at a grid size of 96.5 km (~1° at 30°N/S) and results were
225 qualitatively unchanged. GIS and statistical analyses were carried out in R and PostGIS.

226 Range size weighted richness (rswr) was calculated, for each cell, using the following formula:
227 $rswr_i = \sum_j q_{ij}$ where q_{ij} is the fraction of the distribution of the species j in the cell i .

228 We used ‘Zonation’²⁰ to produce a ranked prioritisation amongst cells, assuming equal weight to
229 all species and assuming an equal cost for all cells. Cell value was the maximum proportion of
230 any species range represented in it. Cell priority was calculated by iteratively removing the least
231 valuable cell and updating cell values²⁰. We analysed all tetrapod species combined and
232 tetrapods without reptiles separately, to reveal the change in rank importance induced by adding
233 reptile distributions (See supplement and Extended Data Fig. 8). We repeated our prioritisation
234 using per-cell agricultural opportunity costs¹⁹, and found via rank correlation that our priority
235 regions are fairly insensitive to the use of land costs (Fig. 4, Extended Data Fig. 8).

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252 AMB, RG, SM, UR conceived the study. RG, CDLO, UR designed the analyses. UR conducted
253 the analyses. AF, SM, MN, UR compiled, designed, and curated the dataset. RG, SM, UR wrote
254 the paper. AA, AMB, MB, RB, BC, FCH, LC, GRC, LD, ID, TMD, AF, LLG, MH, YI, FK, AL,
255 ML, EM, DM, MM, SM, CCN, MN, ZTN, GP, OSGP, DPD, UR, RS, OT, OTC, JFT, EV, PU,
256 PW, YW provided, collated, and verified underlying data. All authors read and commented on
257 the manuscript.

258 UR, AF and MN contributed equally to the paper. RG and SM contributed equally to the paper.

259 **Competing interests**

260 All authors declare no competing interests.

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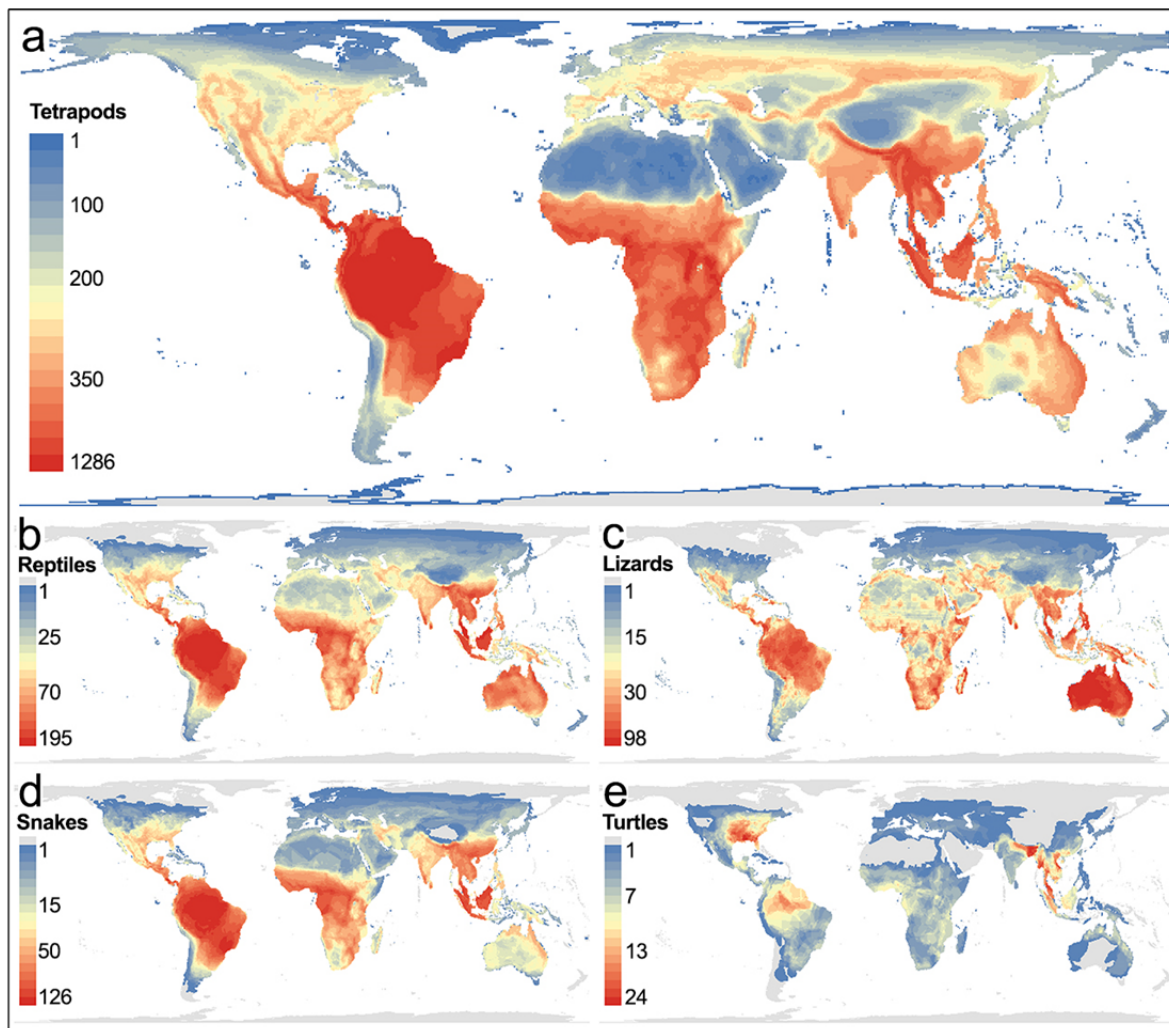
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334 **Figures**

335 Figure 1:



336

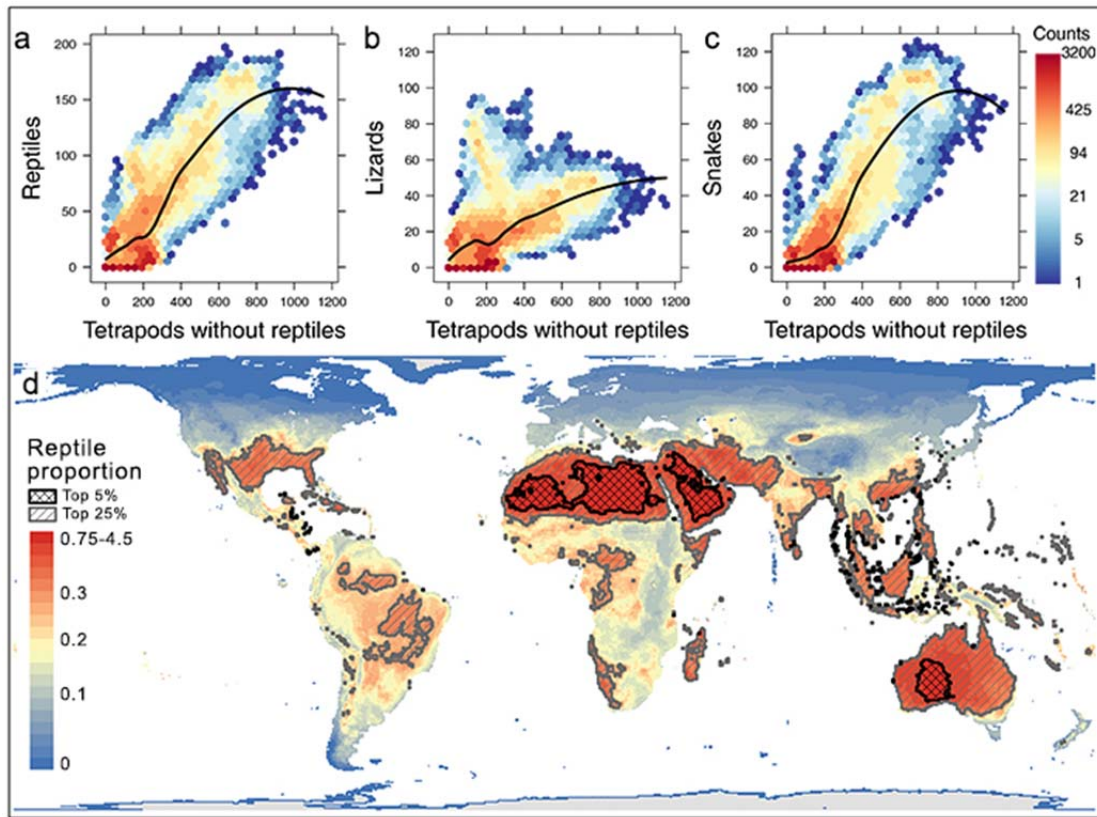
337 Figure 1 – Terrestrial tetrapod species richness maps (0.5° grid-cell resolution). a) all tetrapods
338 including reptiles, b) all reptiles, c) ‘lizards’ d) snakes, e) turtles.

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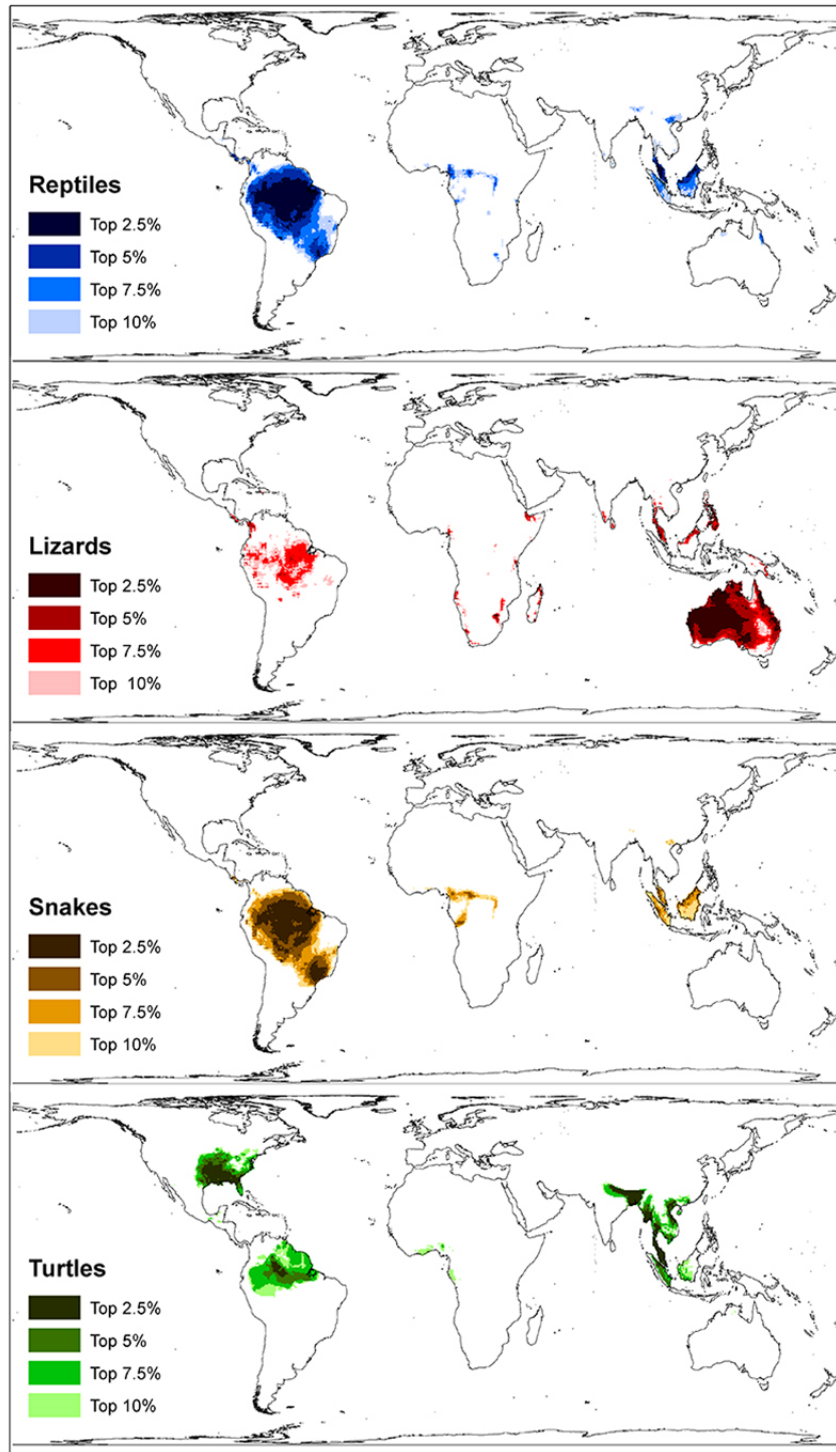
342 Figure 2



343

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

350



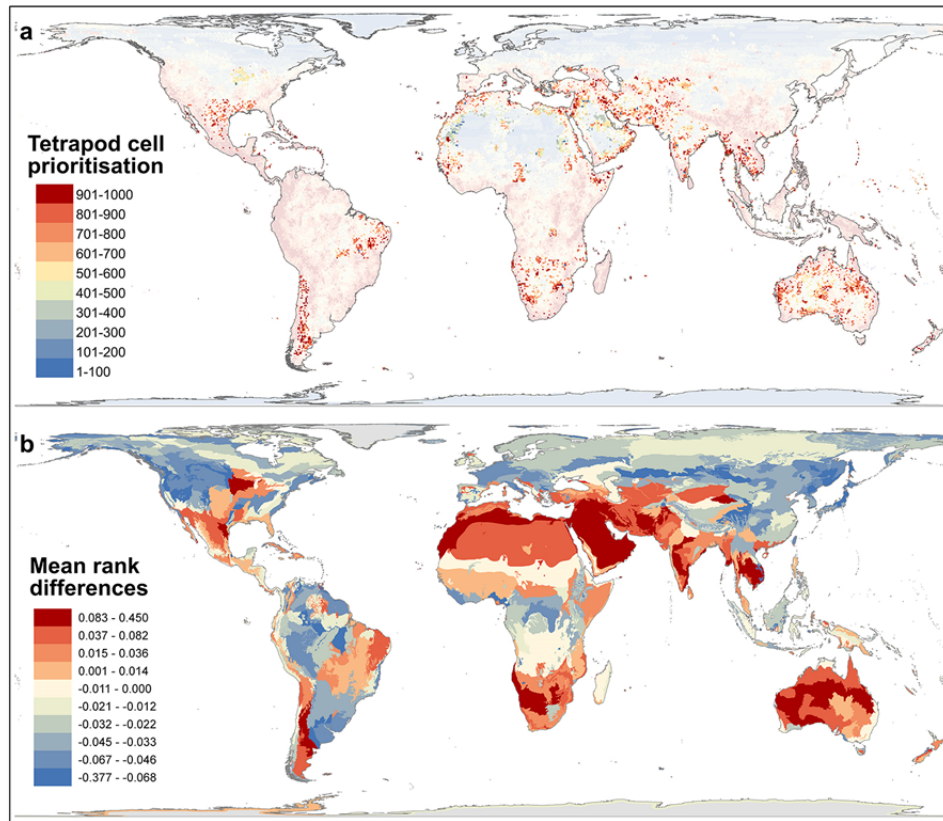
352

353 Figure 3 –Species richness hotspots of reptiles and reptile groups. Those cells that are the 2.5%,

354 5%, 7.5%, 10% richest for a) all reptiles, b) ‘lizards’, c) snakes, and d) turtles.

355

356 Figure 4:



357

358

359 Key areas for tetrapod conservation highlighting regions that increase in importance for
360 conservation due to inclusion of reptiles. Cells were ranked in a formal prioritisation scheme²⁰,
361 based on complementarity when ranking cells in an iterative manner. Cells were ranked twice, I-
362 with all tetrapods, II- with all tetrapods excluding reptiles. a) Patterns per 0.5 degree grid-cell
363 where colours represent the priority ranks for the scheme which included all tetrapods (blue =
364 low, red = high). The cells that are highlighted in bold foreground colours mark regions that gain
365 in conservation importance due to the inclusion of the reptile data. These cells are both (i) in the
366 top 10% of increase in rank, when subtracting the ranks of the analysis with reptiles from the
367 ranks of the analysis without them; and (ii) part of statistically significant spatial clusters of rank

368 changes (using local Moran's I^{30}). b) The mean change in rank between prioritizations with and
369 without reptiles (using the above method), averaged across ecoregions. Red- ecoregions that
370 become more important when including reptiles; blue – ecoregions becoming less important).