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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, for the first time, the global
71 distribution of 10,064 reptile species (99% of extant terrestrial species). We show that richness
72 patterns of the other three tetrapod classes are good spatial surrogates for species richness of all
73 reptiles combined and of snakes, but characterize diversity patterns of lizards and turtles poorly.
74 Hotspots of total and endemic lizard richness overlap very little with those of other taxa.
75 Moreover, existing protected areas, sites of biodiversity significance and global conservation
76 schemes, represent birds and mammals better than reptiles. We show that additional conservation
77 actions are needed to effectively protect reptiles, particularly lizards and turtles. Adding reptile
78 knowledge to a global complementarity conservation priority scheme, identifies many locations
79 that consequently become important. Notably, investing resources in some of the world's arid,
80 grassland, and savannah habitats might be necessary to represent all terrestrial vertebrates
81 efficiently.

82 **Introduction**

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

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

104

105 **Results and Discussion**

106 *Species richness of reptiles compared to other tetrapods*

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

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

121 *Hotspots of richness and range-restricted species*

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

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

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

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

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

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

154 Fortunately, reptiles seem better situated in terms of conservation costs compared to other
155 tetrapods. The median conservation opportunity cost¹⁹ (using the loss of agricultural revenue as a
156 proxy for land-cost) for reptiles is lower than that for other tetrapods ($F_{3, 31850} = 17.4$, $p < 0.001$;
157 Fig. S7). Within reptiles, the opportunity cost is lowest for lizards, and highest for turtles and
158 crocodiles, which could reflect their greater dependence on fresh-water habitats ($F_{3, 10060} = 88.4$,
159 $p < 0.001$; Fig. S7b).

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

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

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

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

183 *Summation*

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 (Figs. 2d, S4). Furthermore, we show that reptiles' unique diversity patterns have important
189 implications for their conservation. Targeted reptile conservation lags behind that of other
190 tetrapod classes, probably through ignorance²⁴⁻²⁶. The distributions provided here could make a
191 vital contribution to bridging this gap. Concentrations of rare species in unexpected locations
192 (Fig. 4) require explicit consideration when planning conservation actions. Highlighting such
193 locations for new taxa could be especially beneficial for resource-constrained planning,

194 especially where land costs are low. The lower global congruence with recognized diversity
195 patterns for reptiles should also serve as a warning sign, contrary to some recent suggestions²⁷,
196 for our ability to use distributions of well-studied groups in order to predict diversity patterns of
197 poorly known taxa. The distinctive distribution of reptiles, and especially of lizards, suggests that
198 it is driven by different ecological and evolutionary processes to those in other vertebrate
199 taxa^{23,28}. The complete distributions of terrestrial tetrapods we now possess could greatly
200 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 Polygonal representations of the extent of species' occurrences, such as we assembled and use in
224 our analyses, are fundamentally important to contemporary conservation planning³⁰. The IUCN's
225 assessment of the extinction risk of individual species requires (and produces) such data, and
226 both they and many other organisations and researchers have used such data in aggregate and at
227 regional-to-global scales for several decades³¹. Like any representation of species distributions,
228 polygonal range maps can include errors both of omission and commission. Both kinds of
229 inaccuracy can lead to erroneous conclusions by unwary users and this has led to some
230 controversy over the use of polygonal range maps. Of course, all biogeographic representations -
231 specimen localities, SDM outputs, atlas data, polygonal maps and explorers' narratives - lie along
232 this omission: commission spectrum, and can equally be misused or found useless³². For global
233 prioritisation, we follow a comprehensive recent study³³ demonstrating the effectiveness of
234 polygonal range maps in highlighting priority areas, despite errors at the level of individual
235 species. We do, however, recognise that specimen data, if collected, curated and made available
236 (at a suitable scale) remains a gold standard for some uses³⁴.

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

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

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

242 $rswr_i = \sum_j q_{ij}$ where q_{ij} is the fraction of the distribution of the species j in the cell i.

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

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266 **Author contributions**

267 AMB, RG, SM, UR conceived the study. RG, CDLO, UR designed the analyses. UR conducted
268 the analyses. AF, SM, MN, UR compiled, designed, and curated the dataset. RG, SM, UR wrote
269 the paper. AA, AMB, MB, RB, BC, FCH, LC, GRC, LD, ID, TMD, AF, LLG, MH, YI, FK, AL,
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271 PW, YW provided, collated, and verified underlying data. All authors read and commented on
272 the manuscript.

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

274 **Competing interests**

275 All authors declare no competing interests.

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279 **Data availability**

280 The reptile distribution data used in this study are available from the corresponding author on
281 reasonable request

282

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365 **Figure captions**

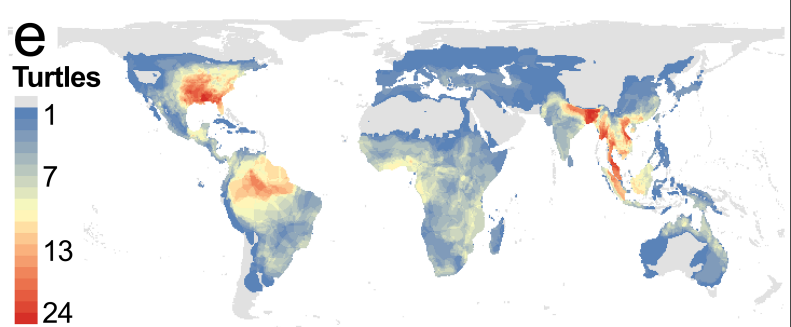
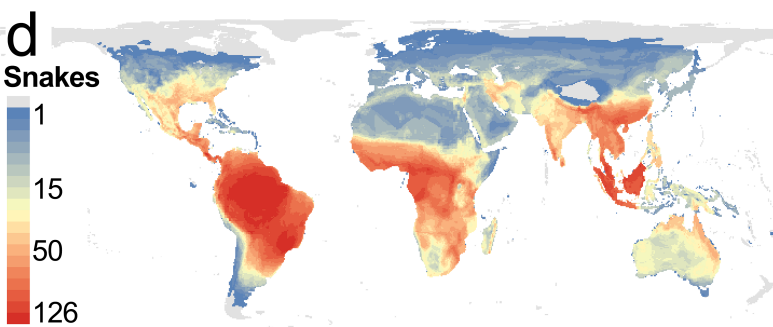
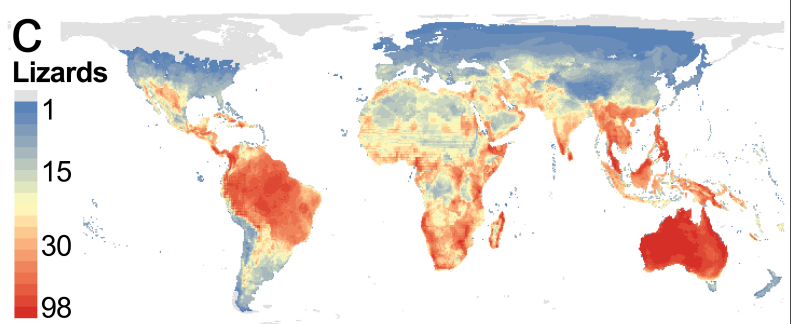
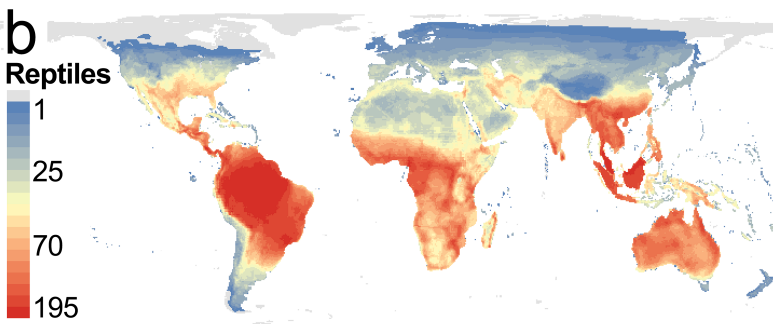
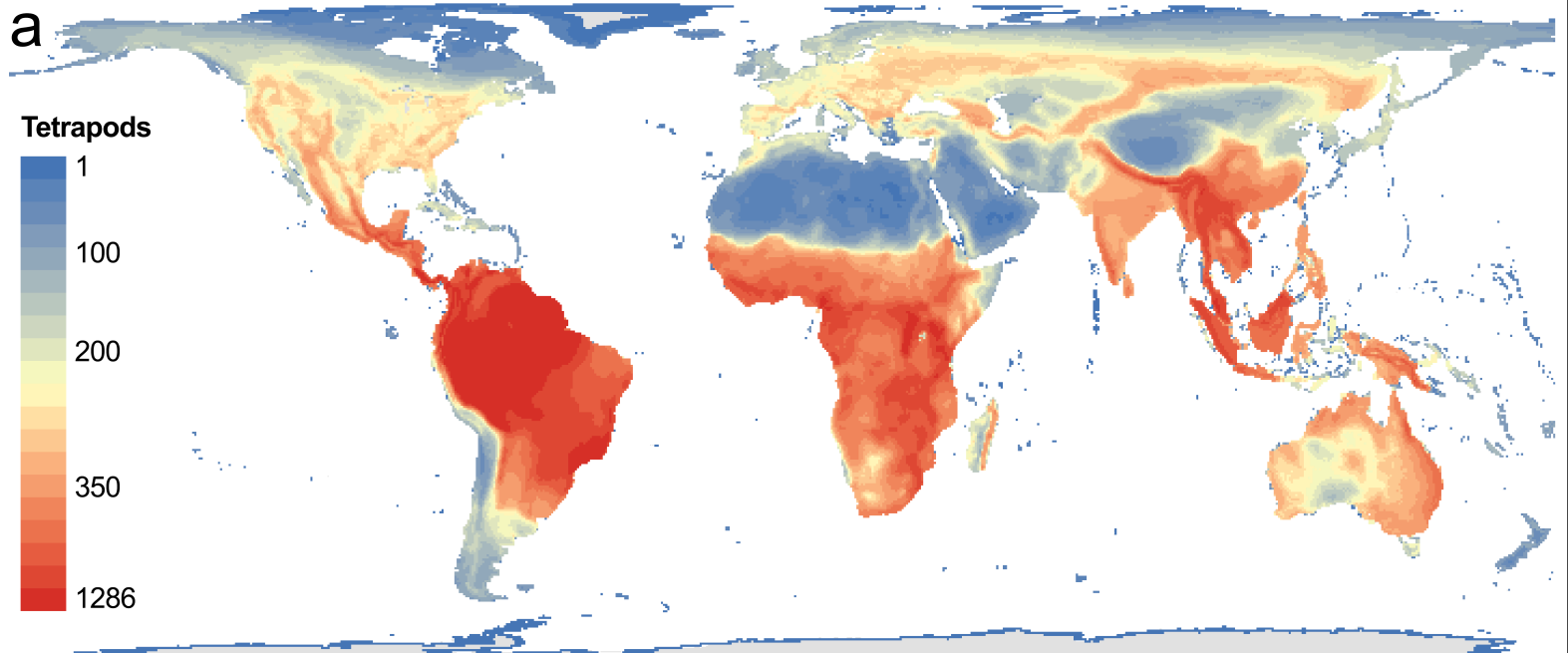
366 Figure 1 – Terrestrial tetrapod species richness maps (0.5° grid-cell resolution). a) all tetrapods
367 including reptiles, b) all reptiles, c) ‘lizards’ d) snakes, e) turtles.

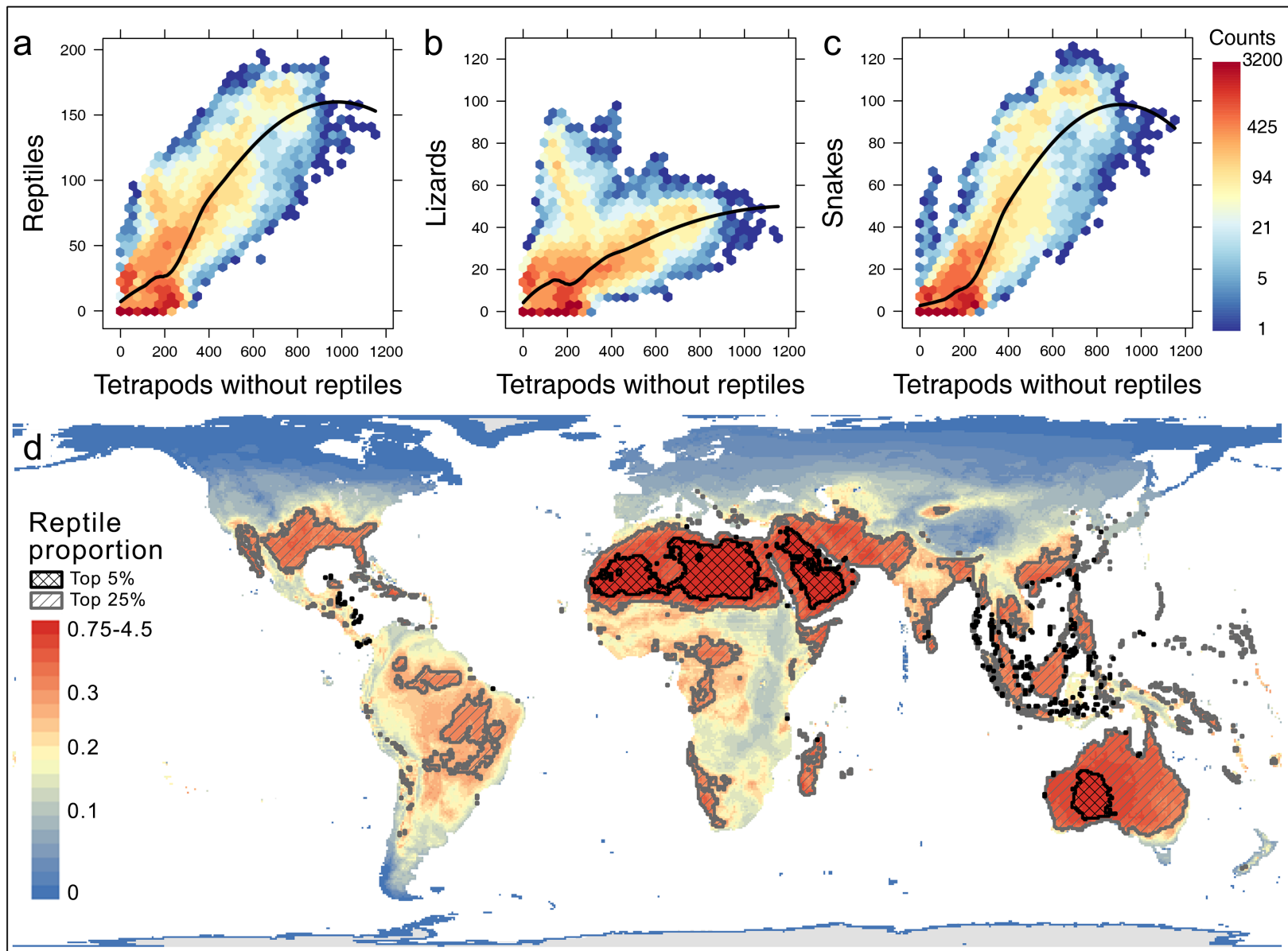
368 Figure 2 – Comparing reptile richness to other tetrapods. Hexagon scatter plots comparing
369 species richness values per grid-cell with binning (black line indicates a loess fit, $\alpha=0.6$) of
370 tetrapods without reptiles, to a) all reptiles, b) ‘lizards’ and c) snakes. d) a map of the ratio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

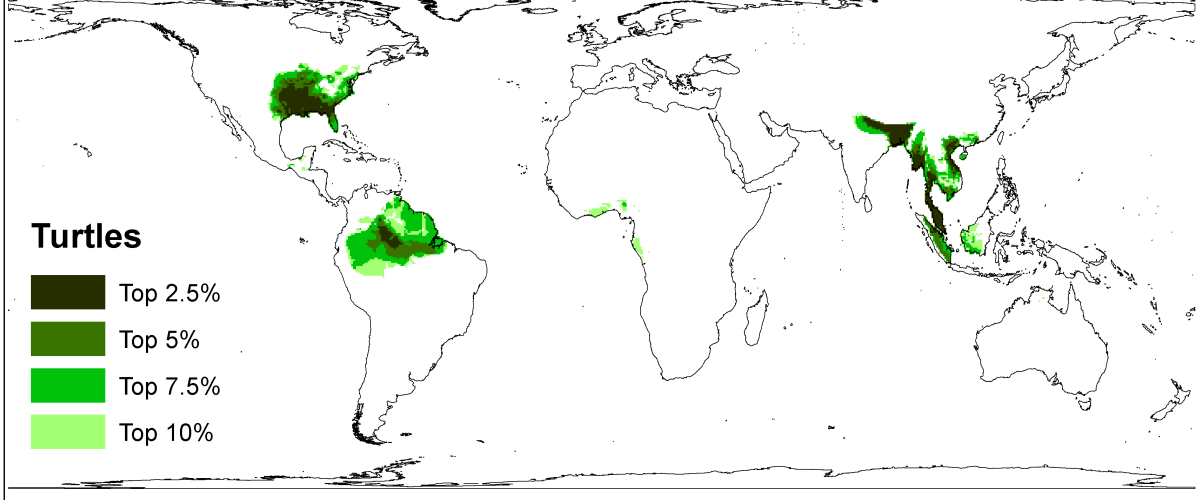
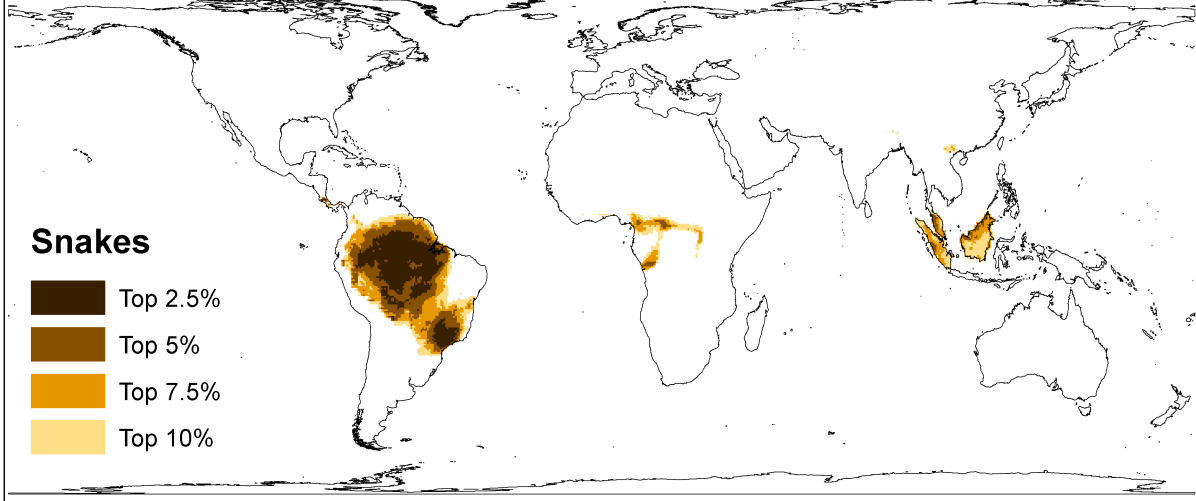
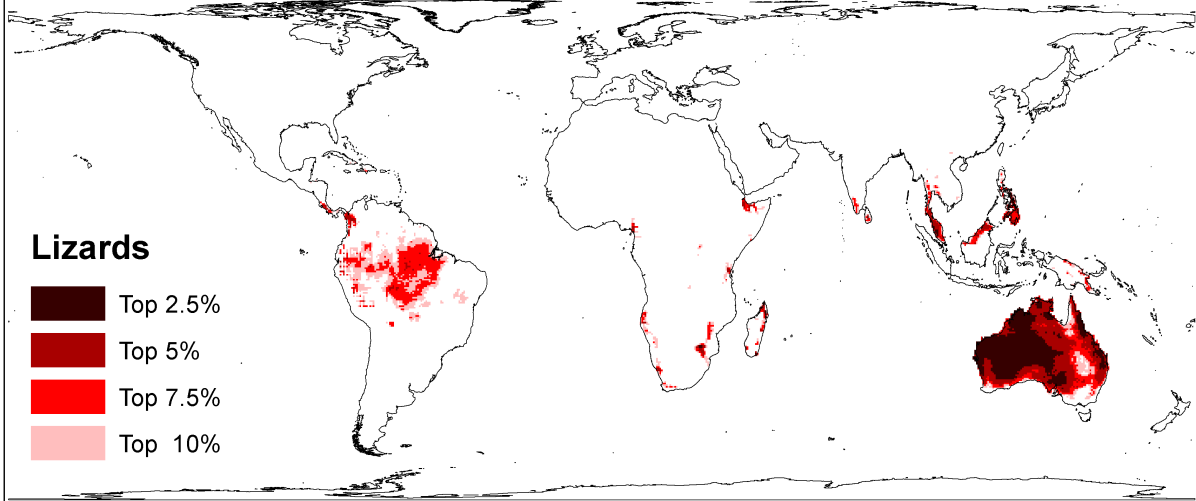
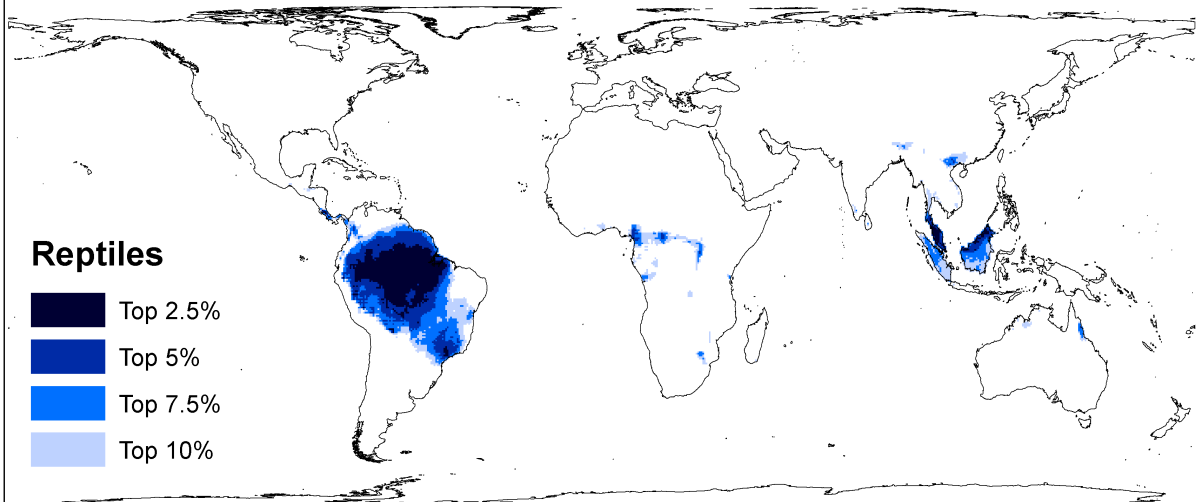
374 Figure 3 –Species richness hotspots of reptiles and reptile groups. Those cells that are the 2.5%,
375 5%, 7.5%, 10% richest for a) all reptiles, b) ‘lizards’, c) snakes, and d) turtles.

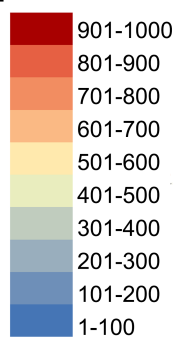
376 Figure 4 – Key areas for tetrapod conservation, highlighting regions that rise in importance for
377 conservation due to inclusion of reptiles. Cells were ranked in a formal prioritisation scheme²⁰,
378 based on complementarity when ranking cells in an iterative manner. Cells were ranked twice, I-
379 with all tetrapods, II- with all tetrapods excluding reptiles. a) Patterns per 0.5 degree grid-cell
380 where colours represent the priority ranks for the scheme which included all tetrapods (blue =
381 low, red = high). The cells that are highlighted with the bold foreground colours are those that
382 pinpoint those regions that gain in conservation importance due to the inclusion of the reptile
383 data. These cells were selected following these two rules (i) they were in the top 10% of increase
384 in rank, when subtracting the ranks of the analysis with reptiles from the ranks of the analysis
385 without them; and (ii) were part of statistically significant spatial clusters of rank changes (using
386 local Moran’s I^{35}). b) The mean change in rank between prioritizations with and without reptiles

387 (using the above method), per ecoregion (red- ecoregions that become more important due to the
388 inclusion of reptile information; blue – ecoregions becoming less important).







a**Tetrapod cell
prioritisation****b****Mean rank
differences**